Visuospatial attention and visual perception in peripersonal space: The impact of intrinsic hand representation and manual action goals

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**Abstract**

Hands have evolved as specialised effectors capable of both fine-tuned and gross motor actions. Thus, the location and functional capabilities of hands are important to defining which visual objects are action-relevant from the multitude of visual information in our environment. Visuospatial attention plays a critical role in the processing of such inputs. The aim of the present thesis was to investigate how internal representation of the hands and the actions we aim to complete with them, impacts visuospatial attention near the body.

In study 1, I investigated how visuospatial attention contributes to luminance contrast sensitivity and object dimension judgements near hands. Targets were presented either briefly (43ms) or for a duration sufficient to facilitate shifts in covert visuospatial attention prior to target offset (250ms). Observers detected onset of visual objects of varying luminance contrasts (Experiment 1) and discriminated the dimension in which rectangles of varying aspect ratios were largest: width or height (Experiment 2) with hands adjacent to or distant from the display. In Experiment 1, for low-contrast stimuli, there was greater accuracy when detecting targets presented for 250ms versus 43ms. The opposite was true for high contrast stimuli: there was greater accuracy when detecting targets presented for 43ms versus 250ms and hand proximity did not modulate either of these effects. For Experiment 2, 250ms target presentations resulted in reductions of the vertical bias in aspect ratio judgements and improvements in visual sensitivity when hands were adjacent versus distant from the monitor. Visual sensitivity for the hand-adjacent posture was also greater for 250ms compared with 43ms target durations indicating enhanced object dimension precision for near-hand objects following shifts in visuospatial attention.

In study 2, I examined how internal representation of the hands (handedness and grasping affordances) influences the distribution of visuospatial attention in peripersonal space. Left and right handed participants completed a covert visual cueing task, responding with either their dominant or non-dominant hand (Experiment 1), with the non-response hand adjacent to one of two target placeholders (and the other responding) either aligned with the shoulder (Experiment 2) or crossed over the body midline in the opposite region of hemispace (Experiment 3). In blocked trials targets appeared near the grasping (palmar) or non-grasping (back-of-hand) region of the hand. Experiment 1 found no evidence for visuospatial biases associated with handedness or response hand laterality. In Experiment 2, right-handers showed a larger attentional cueing cost for objects near the grasping surface versus non-grasping surface of their dominant hand suggesting that visuospatial attention is engaged more rapidly and disengaged more
slowly to objects near the graspable (versus non-graspable) space. Moreover, only hand proximity biases remained when hands were crossed over the body midline (Experiment 3) and were not evident for left-handers. This indicates that visuospatial biases are specific to the functional properties of hands, and to the strength of the underlying representation of the hand.

Finally, in study 3 I investigated the impact of action goals on the distribution of near-body visuospatial attention (Experiment 1) and how the temporal relationship between the non-task relevant visual distractors and targets modifies this (Experiment 2). Following the illumination of either a left or right target light emitting diodes (LED), participants reached to point-to or grasp target objects. Coincident with target onset, a distractor LED illuminated in either the same or opposite visual hemispace halfway between the initiation point and target, or no distractor appeared. In Experiment 1, during grasp reaches there were greater temporal distractor interference effects (slower reach initiation and greater trajectory deviations along the x-axis) compared with point reaches. In Experiment 2, distractor onset was either 200ms prior to (-200ms), coincident with (0ms) or 200ms (+200ms) following the target onset. For both point and grasp actions -200ms distractors resulted in greater interference effects compared with 0ms and +200ms. For grasp reaches +200ms distractors resulted in larger interference effects compared with 0ms and -200ms distractors were associated with more deviated reach compared with coincident and +200ms for pointing actions. Grasp reaches also displayed greater trajectory deviation for -200ms distractors compared with coincident conditions. These findings indicate that grasping remaps the distribution of visuospatial attention such that non-target objects within in the frame of action are prioritised more so than when pointing. Moreover perceptual uncertainty regarding the layout of actable space influences grasping reach trajectories more so than pointing reaches.

The current thesis presents evidence that near-body visual perception is contributed to by a hierarchy of attentional biases associated with functional representation of hands and manual action goals. The results show that near-body visuospatial attention is driven in a bottom-up manner relative to the location and functional properties of hands. Importantly they also provide evidence for concurrent top-down modulations of near-body visuospatial attention, relative to manual action goals which update action to accommodate changes in the visual environment.
Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications included in this thesis

This thesis contains three empirical chapters (Chapters 2, 3 and 4) that contain studies which have been published, submitted or are in preparation for submission at a peer-review outlet. These studies are contextualised with a General Introduction (Chapter 1) and a General Discussion (Chapter 5). Below I list the citation and contributions for each of the empirical articles.


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<th>Contributor</th>
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<td>Hayley A Colman</td>
<td>Conceptualised &amp; designed experiments (80%)</td>
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<td>Data collection, analysis &amp; interpretation (70%)</td>
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<td>Roger W Remington</td>
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Contributions by others to the thesis
Ada Kritikos and Roger Remington were key contributors to this thesis and were involved in the conceptualisation, design and interpretation of experiments, the development of the candidate’s research skills and proof-reading of manuscripts and the thesis as a whole. Simon Watt was integral to the experiment design and data analysis of Chapter 2. David Lloyd contributed to the experiment programming for Chapter 4. Maddison Campbell and Jessica Byrne (research experience undergraduate students) assisted in behavioural data collection on Chapter 4.

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VISUOSPATIAL ATTENTION AND VISUAL PERCEPTION IN PERIPERSONAL SPACE: THE IMPACT OF INTRINSIC HAND REPRESENTATION AND MANUAL ACTION GOALS
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List of Abbreviations

2AFC: Two alternative forced-choice
AB: Attentional blink
AIP: Anterior intraparietal
ANOVA: Analysis of variance
BOLD: Blood oxygen level dependent
cd/m²: Candelas per metre squared
CRT: Cathode ray tube
F5: Ventral premotor area of macaque premotor cortex
Hz: Hertz
IOR: Inhibition of return
LGN: Lateral geniculate nucleus
LED: Light emitting diode
mm: Millimetres
ms: Milliseconds
RHI: Rubber hand illusion
RT: Reaction time
SD: Standard deviation
SE: Standard error
SOA: Stimulus onset asynchrony
SRC: Stimulus-response compatibility
v: Volt
V1: Primary visual cortex
V2: Secondary visual cortex
V4: Extrastriate visual cortex
V-H: Vertical-horizontal
CHAPTER 1: GENERAL INTRODUCTION
From the moment we wake up and fumble to turn off our alarm, we rely on complex perceptual and attentional processes tied to our hands to move about and interact with the objects and people in the world around us. The integration of this information from many different sensory modalities enables us to create an internal representation of both our own body and how our environment is structured around us. This sensory integration (and the resulting internal representations it facilitates) takes the form of perceptual grouping individual sights, sounds, smells, touches and tastes based on their relatedness to one another and their proximity and relevance to the task at hand. Thus, how we plan to use our body to interact with our environment plays a critical role in defining which inputs are related to the task at hand and relevant at any given time. This is particularly the case with regards to our hands, because they are our primary effectors. Hands are the limbs we most often use for object-based interactions and are capable of executing both fine-tuned actions, such as threading a needle as well as gross motor action like swatting away a fly.

A substantial body of evidence suggests that where the body is and what we are doing with it are critically important for the selection and perceptual processing of inputs in our environment. In other words, investigating the interplay between body representation and the perceptual processing is key to understanding how we perceive the world around us. Yet, with regards to hands, there is a disconnect between research focusing on the bottom-up selection and perceptual processing of visual inputs near the body and that investigating how top-down action goals modulate the selective processing of visual inputs. How these processes work in combination with one another is of critical importance because both occur concurrently during manual action. The aim was to present a systematic investigation of the mechanisms involved in guiding manual actions. Specifically, how proximity to the hand modulates bottom-up perceptual and attentional processes and in turn, how top-down goals modulate bottom-up processing. To do this, I drew upon concepts from three of the major theories of perception and action: the two visual pathways, integrative and embodied theories of cognition.

**Prevailing theories of perception and action**

A number of separate but interconnected mechanisms contribute to near-body visual processing (Goodale & Milner, 1992; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). The common link between them is that they are intrinsically linked to the body both with regards to representing sensory information relating to limb location (visual, tactile and proprioceptive) and how we plan to use our body to act upon objects in our world (action goals). Neural systems dedicated to representing the body parts interface with those which select relevant
environmental inputs to guide the planning and execution of manual actions (Goodale & Milner, 1992).

Actions we plan to complete shape our perceptual experiences of the world around us, and in turn our experiences of the world around us shape how we plan our actions. Thus, the core premise underlying most theories of perception and action is that perceptual processing is critical for action, and as a result action modulates perceptual experience (Gibson, 1979). There are fundamental differences between theories, however. The two visual pathways theory (Goodale & Milner, 1992), proposes that general visual perception and perception for action are independent from one another. Alternatively, the integrative theory (Prinz, 1990) and embodied cognition (Decety & Grèzes, 2006) focus on the bidirectional relationship between perception and action. The latter two theories posit that perception exists to facilitate action, so evaluation of perception provides insights about action and vice versa. In the present thesis I draw upon each of the theories described below to evaluate the interplay between hand representation and attention.

**The two visual pathways theory.** This theory distinguishes between visual processing for perception and visual processing for action, subserved by the ventral and dorsal visual stream respectively. The ventral visual pathway deviates from V1 through V2 and V4 and terminates in the inferotemporal cortex (Ettlinger, 1990; Mishkin & Ungerleider, 1982; Schneider, 1969). Early understanding of ventral processing proposed that it was responsible for the selective processing of visual inputs relevant to object awareness: or the ‘what’ elements of object processing (Goodale, Ingle, & Mansfield, 1982). By comparison, the dorsal visual stream deviates from V1 through the occipital cortex and terminates in the posterior parietal (Goodale, et al., 1982) and was thought to be responsible for processing visual information required for localising objects: the ‘where’ elements of object processing, (Goodale, et al., 1982; Mishkin & Ungerleider, 1982).

Goodale and Milner’s (1992) subsequent ‘separate visual pathways’ theory revised this model and proposed that the ‘what’ ventral stream is involved primarily in processing visual inputs required for object awareness and discrimination. Conversely, the reconceptualised dorsal ‘how’ stream is responsible for processing visual inputs required for visuomotor control. That is, the dorsal stream selectively processes visual inputs related both to where an object is located as well as recruiting visual inputs to guide actions. In this way the theory differentiates between perceptual awareness of space and action-based space processing.

Evidence from clinical neuropsychological research is used to support this dissociation of object identity processing from and action-relevant visual processing
Case studies of patient DF, a sufferer of visual form agnosia following damage to occipital-temporal cortex (in the ventral visual stream), show deficits in object recognition but intact visuomotor abilities (Carey, Harvey, & Milner, 1996; Goodale, Milner, Jakobson, & Carey, 1991). While unable to identify the dimensions of objects, DF was able to match the orientation of a slot with a card when posting it through the slot (intact visually guided action abilities) as well as effectively identifying the axes of symmetry on novel objects; a requisite for successful grasping-to-lift (Carey, et al., 1996; Goodale, et al., 1991; Milner et al., 1991). Convergent evidence from patients with optic ataxia following damage to the superior parietal in the dorsal stream suggests that individuals with intact ventral and impaired dorsal processing can perform object recognition and discrimination tasks but not execute goal-directed reaches reliably (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003). Consistent with the two visual pathways theory, these findings indicate that ventral visual steam lesions results in deficits in object recognition whereas dorsal visual stream lesions result in deficits in using visual information to guide action.

These findings provide evidence for dissociation in the processing of specific types of visual inputs, based on their differential relevance to perception for awareness, versus perception for action. Critically, they provide direct links between the neurological infrastructure required for processing action-relevant visual inputs and the behavioural consequences of action. I draw upon behavioural methodologies used to evaluate the two visual pathways theory, to examine the influence of visual attention on visual perception in the space near hands. Specifically, I examine how hand proximity modulates the processing of dorsal visual inputs (Chapters 2 and 3).

The two visual pathways theory focusses on the role that visual objects play in guiding manual actions, yet in the present thesis I was also interested in investigating how the actable properties of the body and the goals of actions themselves, shape the selection of action relevant visual and non-visual stimuli in the environment. The integrative and embodied cognition theories of perception and action focus on the bidirectional relationship between environmental stimuli and bodily states, and I drew upon them in the present thesis to examine how the actable properties of hands and action goals modulate environmental processing.

**The integrative theory.** The integrative theory extends on the two visual pathways theory by focusing on the bidirectional relationship between perception and action. Namely, how action goals shape visual perception and in turn how visual perception shapes how a given action is executed. The theory is fundamentally grounded in the common coding hypothesis and is based on evidence from research on perception-action
coupling. The common coding posits that intentional control occurs either simultaneous with, or prior to informational control of action (Prinz, 1990). That is, rather than movements being perceptually processed in terms of their output (such as kinematics/muscular contraction etc.), environmental stimuli are perceptually processed relative to preceding or planned actions (Frese & Sabini, 1985). Thus, the integrative theory is grounded in the concept that performing an action results in a bidirectional association between the motor output it has generated and the sensory input from the environment that arise after an action (Hommel, Müßeler, Aschersleben, & Prinz, 2001). In other words, subsequent actions are adapted to match the preceding environmental input.

Retrieval of this association between perception and action can be used to predict future effects of actions and also be applied to the actions of others during action observation (Humphreys et al., 2010). Prism lens adaptation presents an example of such adaptation. This is characterized by motor system adaption to new visuospatial coordinates following exposure to prisms which displace the visual field. Critically, once exposure to the prisms ceases, the actor displays demonstrable aftereffects before adapting motor behaviour to successfully interact with objects (Fernandez & Bootsma, 2004). This adaptation and subsequent aftereffects provides evidence for this perception action coupling.

More recent conceptualisations of this theory propose that perception-action coupling provides a pre-reflexive understanding of biological actions that match their own action catalogue (Gallese, Rochat, Cossu, & Sinigaglia, 2009). Further behavioural evidence for such perception-action coupling comes from studies of blind walking which demonstrate that motor output is adapted to match the incoming visual information. Specifically, there is evidence for the recalibration of perception-action coupling after neurotypical observers are exposed to a mismatch between visual self-motion inputs and associated biomechanical self-motion inputs (Reiser, Pick, Ashmead & Garing, 1995). In the blind walking task, the actor must walk with eyes-closed to a previously viewed target location on the ground. In the adaptation phase the actor is presented with environmental flow information that mismatches (is either faster or slower) than actual walking speed. Following ongoing exposure to mismatched visual environment information, blind walking performance results in either undershooting or overshooting of the target (relative to the prior to adaptation stage) when the visual flow information in the exposure phase is faster or slower respectively (Reiser, et al., 1995).

These findings provide evidence for perception-action coupling because they suggest that when perceptual inputs from the environment are incongruent with body-centred action related sensory inputs, subsequent actions are adapted to fit the changed
environment. Thus, actions are adapted in response to the perceptual consequences of preceding action. This perception-action coupling link is critical to the current thesis because it suggests that the link is updated dynamically to accommodate changing requirements. Accordingly, when an observer is acting in a dynamically changing environment, there is an ongoing interplay between perception and action to facilitate effective object interactions. This is investigated in the present thesis (Chapter 4) where I examine how action goals and changes in the visual environment shape the distribution of visuospatial attention within the immediate environment.

**Theory of embodied cognition.** Embodied cognition may be regarded as an extension of the integrative theory and similarly proposes that our representations, including both lower level perceptions and higher level thoughts, are bounded by bodily states and the sensory motor system (Creem-Regehr & Kunz, 2010). This is such that goal directed actions alter perception of the environment. In turn, subsequent perceptual events are coded in relation to the preceding goal-directed actions. Thus, the embodied perspective is also consistent with the common coding hypothesis in that how we use our body to interact with our environment shapes how we process and attend to sensory stimuli in our vicinity (Barsalou, 2008; Bridgeman & Tseng, 2011; Reed, McGoldrick, Shackelford, & Fidopiastis, 2004). It extends upon the integrative theory by proposing that representation of the actable properties of the body itself and of objects, for example the ‘graspability’ of objects near hands, also modulates perceptual processing and subsequent action (Reed, Betz, Garza, & Roberts, 2010).

The theory of embodied cognition is also based on the premise that the processes involved in action planning and execution are also involved in representing the actions of others (Decety & Grèzes, 2006). Neurophysiological research provides strong evidence for this, in particular the discovery of the action-observation or ‘mirror’ neuron system (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Rizzolatti et al. (1996) identified such mirror neurons in area F5 of the macaque premotor cortex, which displayed activations for both tasks which involved executing an action, and when the observer viewed another actor execute the same action (Rizzolatti & Craighero, 2004; Rizzolatti, et al., 1996).

Subsequent investigations have revealed that the mirror neuron system is critical to our understanding our own actions, the actions of others and in our ability to imitate other’s actions (Decety & Grèzes, 2006; Rizzolatti, et al., 1996). This is the case for both seen and unseen actions. For example activation is also found when the primate only hears the consequences of the action (e.g. the sound of ripping paper) as well as when the primate executes the same action (Kohler et al., 2002). The analogous mirror network in humans,
identified by functional imaging studies in the inferior parietal and parts of the premotor cortex, shows similar activation (increased BOLD response) for both one’s own imagined actions as well as when viewing of actions of others (Decety & Grèzes, 2006). Evidence from the same study also reveals that the temporal-parietal junction is involved in this mirror network, specifically in relation to assigning agency: discriminating one’s own actions from the actions of others.

Behavioural evidence from tool-use research provides further insights into the embodiment of cognition, because findings suggest that tool-use changes the functional representation of the body. In their seminal study, Iriki, Tanaka and Iwamura (1996) trained rhesus macaques to use raking tools to complete simple actions. The authors found that the visual receptive fields of neurons in the caudal postcentral gyrus that coded for the hand during manual actions remapped to include the entire length of the rake during tool actions. These findings indicate that using a tool changes the internal representation of the confines of the body such that the tool is represented as part of the body for the duration in which we use it (Berti & Frassinetti, 2000; Maravita & Iriki, 2004).

Finally, object affordance research provides convergent evidence for the embodied theory because it suggests that the properties of objects themselves facilitate motor actions. Tucker and Ellis (1998) illustrated this in their now classic study of object action affordances (though see Cho and Proctor (2010) and Bub and Masson (2010) for an alternative explanation of these effects). Participants completed a stimulus-response compatibility task in which they responded by key press to images of objects that were action congruent (e.g. the handle of a saucepan oriented towards) or action incongruent (e.g. handle oriented away) from the hand making the response. Responses were significantly faster to action congruent than action incongruent objects (Tucker & Ellis, 1998a). Recent electrophysiological research provides evidence for the embodiment of object affordances prior to action. Goslin et al. (2012) recorded event related potentials during a stimulus-response compatibility task and found greater lateralised rapid motor preparation for the hand afforded by the object orientation. Importantly, motor preparation (lateralised readiness potentials) occurred around 400ms prior to action execution which suggests that vision and action binding occurs early in the sensory pathways. Both described findings provide evidence for the embodiment of perception because they show that how the body acts upon the object in question modifies early visual processing.

Taken together, the above findings suggest that the functional capabilities or ‘actable’ properties of objects that we interact with not only shape but also facilitate certain action programs. Moreover, they indicate that we adapt the internal representation of our
own physical body to incorporate the functional properties of tools. In this way, the embodied theory of cognition extends on the integrative theory by proposing that perceptual events are not only coded in relation to the preceding action and vice versa, but that intrinsic factors such as the biomechanics of the body and the physical properties of objects also shape how perceptual events are represented. We draw on this in the present thesis to investigate how the internal representation of the body shapes near body visual processing. Specifically, I examine how the biomechanics of the hand influence the way that attention is directed to objects near the body, and conversely how action goals also shape visual attention.

Representing the body

The described theoretical accounts, draw upon an established body of research which has shown that the sensory representation of the body is systematically linked with cognitive and attentional processing. Body schema and peripersonal space are two concepts which are critical to understanding this link between perception and action. Substantial evidence suggests that they are intrinsically linked because both have substantial impact on the representation and perceptual processing of body-centred sensory inputs (Berlucchi & Aglioti, 1997; Graziano, 1999; Holmes & Spence, 2004; Rizzolatti, et al., 1981). Moreover, they are adaptable and change with the perceptual environments in such a way as to best facilitate action. As a result, quantifying perceptual patterns attributable to body schema and changes to the representation of peripersonal space, are some of the primary ways to investigate the relationship between perception and action.

Body schema. The term body schema refers to the united percept of the body and its movements (Berlucchi & Aglioti, 1997). It reflects both the neural representation of the body as well as conscious ownership and volitional control of the body itself (Berlucchi & Aglioti, 1997; Maravita & Iriki, 2004). Holmes and Spence (2004) postulated that body schema and representation of peripersonal space are subserved by interconnected neural networks that monitor, from a body centred frame of reference, the location of events and objects in space. This representation of the body relies on the systematic integration of proprioceptive, vestibular, visual and tactile inputs as well as visual perception of the structure and movements of the body (Berlucchi & Aglioti, 1997; Cardinali et al., 2009). Thus, maintaining internal representation of the body, and in particular the hands, strongly depends on the continuity between proprioceptive, visual and tactile inputs. Behavioural studies of neurotypical subjects indicate that disruptions to the continuity of multisensory
inputs results in distortions to body schema (Costantini & Haggard, 2007; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004). One way that this has been demonstrated is using the rubber hand illusion (RHI) which is characterised by feelings of ownership or agency over a rubber hand following synchronous stimulation of both one’s actual (unseen) hand and the visible rubber hand (Botvinick & Cohen, 1998). As well as subjective reports of feelings of ownership, observers also demonstrate distortions of judgments of perceived hand location that shift towards the location of the rubber hand and away from the hand’s physical location. The illusion reflects the role of sensory concordance in body schema because congruence (or synchrony) between visual and tactile inputs is required for the illusion to occur and particularly for the presence of subjective feelings of ownership and agency over the rubber hand (Holmes & Spence, 2005). Moreover, similar to blind walking experiments these results demonstrate that visual inputs are weighted most highly in perceptual processing when it comes to localising both the body itself and objects near the body.

**Peripersonal space.** Conceptualisations of peripersonal space are causally linked with those of body schema because they arise from the same perceptual processes (Holmes & Spence, 2004). Peripersonal space refers to the space near the body within which we manipulate objects. Specifically, it refers to the spatial field that falls within 30cms around given body part, for example, the hand. Peripersonal space is distinct from extrapersonal or ‘far’ space, which encompasses space outside of this zone (Holmes & Spence, 2004). In addition, representation of the space near the hand tapers in a graded way such that sensory inputs which arise from the location directly on or next to a given body part, are subject to greater perceptual prioritisation than those ~ 30cms from the body part (Longo & Lourenco 2006, 2007). Multisensory integration is critical to peripersonal space. Spatially and temporally coincident stimuli from multiple sensory modalities are integrated and processed as belonging to a single perceptual event or object when they occur within peripersonal space. Peripersonal space is distinguished from extrapersonal space by the way that spatially and temporally concurrent stimuli from multiple sensory modalities are combined and perceptually processed as belonging to a single perceptual event or object (Stein & Stanford, 2008). Whilst multisensory integration still occurs in extrapersonal space, it occurs to a greater extent (particularly in regards to visual and tactile inputs) for objects and events within peripersonal space. Evidence from single cell recordings in cats (Meredith, Wallace, & Stein, 1992) and rhesus macaques (Iriki, et al., 1996; Rizzolatti & Craighero, 2004) indicates that firing of bimodal neurons (neurons that respond to inputs from two or more sensory modalities) is strongly
dependant on the spatial proximity of the stimuli to the body. That is, integration is enhanced for sensory stimuli which occur on or within thirty centimetres of the body (Stein, 1992). Importantly, representation of peripersonal space is flexible such that it remaps with the location of hands (and body) in space (Graziano, Yap & Gross, 1994). That is, peripersonal space is specific to the hands location. Visual receptive fields move with the hands when they are extended out into space or crossed over the midline of the body to prioritise the region most likely to contain action-relevant sensory inputs (Maravita, Spence, & Driver, 2003).

Behavioural evidence for representation of peripersonal space in humans comes from crossmodal congruency tasks. In such tasks, participants typically make speeded (manual, foot-pedal or saccadic) responses to a target from one sensory modality whilst presented with a distractor in another modality (most typically using visual-tactile or auditory-visual pairings). In the visual-tactile version of the task participants receive tactile stimulation of the thumb and forefinger (which comprise the lower and upper locations) of both hands whilst presented with visual (LED) distractors at the same upper and lower locations. Targets and distractors are temporally coincident (presented within 50ms of one another) and spatially congruent (e.g. both occurring in the upper location) or incongruent (e.g. tactile stimulation of thumb and visual stimulation near forefinger) irrespective of hand. Results suggest that observers are faster (and make fewer errors) when responding to congruent versus incongruent bimodal stimuli (Kennett, Spence, & Driver, 2002). Critically, this bimodal congruency effect is largest if both distractor and target are on the same hand which suggests that bimodal stimuli are integrated and thus perceived as arising from a singular event or object (Macaluso & Maravita, 2010; Stein, 1992).

The findings from the crossmodal congruency task is consistent with single-cell recordings in indicating that peripersonal space remaps with the location of the hands in space (Maravita, Spence, Kennett, & Driver, 2002). More than this, subsequent findings from the same paradigm suggest that vision of the body part is not required to facilitate multisensory integration - peripersonal space maps with unseen hand location. Kennett, Spence and Driver (2002) investigated this using a tactile target-visual distractor crossmodal congruency task and participants with unseen hands, uncrossed or crossed over the body midline. Tactile discrimination performance was significantly better when a visual distractor was presented on the same side (versus opposite side) as the unseen hand (Kennett, et al., 2002). This suggests that intrinsic (non-visual) representation of the body’s location is sufficient to facilitate integration. The present thesis extends upon this work to examine the bidirectional relationship between the sensory representation of the
Body on the one hand and on the other, mechanisms of visuospatial attention which facilitate further cognitive processing of action relevant inputs.

**Body-centred mechanisms of visual attention**

Evidence from attention research suggests that the distribution of visuospatial attention is bi-directionally related to multisensory integration. Specifically, multisensory events or objects may shift visuospatial attention to their location, whilst top-down action goals can shape the way that attention is distributed near the body to facilitate multisensory integration at the site of action.

**Bottom-up attention processes.** Attention can be captured by objects near the body exogenously (without voluntary control), based on their perceptual salience. In the context of action near-body stimuli, such inputs may relate to objects which may be obstacles to planned actions or may represent a new object upon which one may want to act. Thus, a goal object’s proximity and intentional value to the body modulates perceptual ‘saliency’ (Talsma, et al., 2010). Multimodal inputs in particular are effective at driving bottom-up shifts in spatial attention because they provide such environmental cues (Meredith, et al., 1992; Theeuwes, 1991). That is, the presentation of unimodal (especially visual) and multimodal stimuli may drive shifts of attention to their spatial location.

This is supported by evidence from Santangelo and colleagues (2007; 2009) who found that multisensory cues near the body capture spatial attention more easily than unimodal cues and irrespective of perceptual load (the amount of attentional resources required for processing a stimulus). When observers performed up-down discriminations of visual, auditory or auditory-visual stimuli under a no-load condition (no current task) or high load condition (whilst identifying target digits in a rapid central stream of letters), they displayed optimal capture for multimodal stimuli. In the no-load condition both unimodal and bimodal stimuli captured spatial attention, but in the high-load condition only bimodal stimuli successfully captured spatial attention. Further to this, attentional prioritisation of multisensory stimuli is reflected in the representation of peripersonal space. Stimuli occurring on or near the body are not only more likely to be integrated but also to influence shifts in attention irrespective of sensory modality (Macaluso, Frith, & Driver, 2000; Spence, 2002; Spence & Santangelo, 2009). This is evidence that sensory representation of the body, drives shifts in spatial attention.

**Top-down processes.** In contrast to sensory representation driving shifts in spatial attention, how we aim to interact with our environment also influences the distribution of attention near the body. Specifically, top-down attention is shifted to objects in near body
space relative to the action goals of the observer (Baldauf, Wolf, & Deubel, 2006; Tipper, Howard, & Houghton, 1998). Such endogenous shifts of visuospatial attention are essential for the execution of action because they result in the biased distribution of visuospatial attention towards the goal objects as well as those which may influence our planned action (Talsma, et al., 2010). Specific evidence for this comes from findings that visual inputs falling within the space of action are prioritised in attention, irrespective of whether they are targets or non-target distractors (Baldauf, et al., 2006; Tipper, et al., 1998). For example, Beldauf and Deubel (2006) found that when observers reached to two or three locations whilst completing an two alternative forced-choice task, number/ letter discrimination was improved for targets presented between the reach targets. This suggests that visual attention was distributed to all target locations during action preparation in parallel rather than serially. These and similar findings indicate that visual attention is distributed near the body relative to the goals of actions so as to facilitate processing of relevant stimuli.

**The current thesis**

Taken together, the above evidence suggests that where the body is and what we are doing with it are critically important for the selection and perceptual processing of inputs in our environment. Moreover, these factors modify visual processing via both bottom-up and top-down mechanisms of attention. Thus, understanding how bottom-up and top-down processes work either in combination or parallel to one another, is critical to understanding the bidirectional relationship between perception and action.

In the current thesis I focussed specifically on manual actions and perceptual and attentional mechanisms involved in processing inputs in near-hand (perihand) space. Perihand space was of particular interest because hands are our primary effectors which we use to reach out, grasp and manipulate objects near our body. The structural and functional morphology of our hands has evolved over millennia to allow the execution of both fine-tuned and gross motor responses (Fernandez & Bootsma, 2004; Nordin & Frankel, 2001). Moreover, the location and movement of the hands, defines the boundaries of peripersonal space and the neural representation of the hands and of manual actions are subserved by the largest proportions of each of the somatosensory, motor and premotor cortices (Bolognini & Maravita, 2007; di Pellegrino, Ladavas, & Farne, 1997; Iwamura, Iriki, & Tanaka, 1994; Rizzolatti, et al., 1996; Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995). Recent evidence suggests that the space directly surrounding the hands is subject to distinct perceptual biases, beyond those found for
general peripersonal space (Gozli, West, & Pratt, 2012). Specifically, the perceptual processing of certain types of visual inputs, such as those relevant for sensorimotor transformations, are enhanced whereas other types, such as those related to object identity discrimination, are suppressed or impaired (Davoli & Brockmole, 2012; Goodhew, Fogel, & Pratt, 2014; Goodhew, Gozli, Ferber, & Pratt, 2013; Gozli, et al., 2012). These findings are critical because they provide further evidence for attentional and perceptual changes within perihand space facilitate perception for action.

The current thesis will draw on constructs from the three major theories of perception and action to examine the question: how is perceptual processing of the space near the hands modified by intrinsic factors relating to representation of hands and manual action goals? To answer this, I will be focussing on three aspects of near hand visual processing, how hand proximity modulates visual sensitivity to different types of visual inputs (Study 1), how the intrinsic factors of handedness and graspability modifies shifts of visual attention in peripersonal space (Study 2) and how manual action goals modify action profiles and the distribution of visual attention to objects in peripersonal space (Study 3).
References


CHAPTER 2: SHIFTS IN VISUOSPATIAL ATTENTION ENHANCE SIZE DISCRIMINATION BUT NOT CONTRAST SENSITIVITY
Abstract
We investigated how shifts in visuospatial attention contribute to near-hand enhancements in visual sensitivity for magnocellular visual properties. Specifically we examined the impact of hand proximity and attention shifts on luminance contrast sensitivity. This was motivated by the prediction that visual sensitivity to complex magnocellular properties relevant to the execution of manual action (such as size discrimination for grip scaling) would be enhanced when visuospatial attention could be shifted to the near-hand targets prior to target offset. By contrast, we predicted that simplified magnocellular properties (such as luminance contrast sensitivity for object localisation) would be sensitive to hand proximity but minimally influenced by shifts in attention. We manipulated covert attention by presenting targets either briefly (43ms) or for a duration sufficient to facilitate shifts in covert visuospatial attention (250ms). In Experiment 1 participants detected the onset of visual objects of varying luminance contrasts with their hands adjacent to or distant from the display. Targets varied in luminance contrast and were high or low contrast or sub-threshold. For low-contrast stimuli, there was greater accuracy when detecting targets presented for 250ms versus 43ms. The opposite was true for high contrast stimuli, there was greater accuracy when detecting targets presented for 43ms versus 250ms. Importantly, hand proximity did not modulate these effects. Experiment 2 investigated visual sensitivity for size judgements. Target were high contrast rectangles that varied in aspect ratio. When targets were presented for 250ms, the vertical bias in aspect ratio judgements was reduced and visual sensitivity to object dimension changes was enhanced when hands were adjacent versus distant from the monitor. Moreover, there was greater visual sensitivity for the hand-adjacent posture when the target was presented for 250ms compared with 43ms. These findings provide novel evidence for perceptual facilitation of near hand visual processing for magnocellular properties relevant to grip scaling. In addition, they indicate that such visual enhancements are contributed to by shifts in visuospatial attention.
Visual information plays a critical role in guiding manual actions. A growing body of research suggests that processing of magnocellular stimulus properties is enhanced in the space near the body (within 30cms of hands) (Chan et al., 2013; Goodhew, et al., 2014; Gozli, et al., 2012). Such enhancement is thought to reflect perceptual prioritisation of the ‘actable’ visual properties of objects such as location and size, and result from selective recruitment of the dorsal visual network (Cosman & Vecera, 2010; Goodhew, et al., 2014; Goodhew, et al., 2013; Reed, Grubb, & Steele, 2006). Importantly, there are near-hand attentional biases which are not restricted to visual inputs; evidence suggest there is crossmodal and non-visual biases in the engagement and shifting of attention. For example, there are improvements in auditory localisation and changes to the temporal and spatial shifts in attention in the absence of visual inputs within the perihand zone (Brown, Kroliczak, Demonet, & Goodale, 2008; Tseng, Yu, Tzeng, Hung, & Juan, 2014). As such, magnocellular enhancement cannot account for enhancements in near-hand perceptual processing entirely, because the dorsal visual pathway deals only with visual inputs. Such changes in non-visual near-hand perception suggest that there are additional (likely attentional) mechanisms which contribute to near-hand processing. This then presents the possibility that such higher-order biases in attention may drive magnocellular visual enhancements rather than lower level differences in perceptual sensitivity driving attentional biases. In the present study we investigated this by examining the additive impact shifts of visual attention to near-hand visual processing. In particular, we investigated whether such shifts drive or enhance magnocellular perception near the hand, compared with when shifts of attention are minimised prior to object-based visual judgements.

A growing body of neurophysiological, neuropsychological and behavioural research has shown that the dorsal (but not ventral) visual pathway is selectively involved in near hand visual perception (Denison & Silver, 2012; Goodhew, et al., 2014; Gozli, et al., 2012). Specifically, the dorsal visual stream is involved in processing of action-relevant magnocellular visual inputs. In line with this, the dorsal pathway is conceptualised as the perception-for-action visual pathway because visual object properties used for guiding actions are selectively processed within this stream. Neuropsychological evidence indicates that magnocellular inputs, and the dorsal visual stream play an important role in guiding manual action. Patients with damage along the dorsal visual pathway display impairments in the localisation of, and ability to reliably execute reaches towards visual targets. Such patients are unable to scale their grip appropriately, identify axes of symmetry on objects or direct reaches to target locations. (Derrington & Lennie, 1984;
Goodale & Milner, 1992; Legge, 1978; Maunsell, et al., 1999; Perenin & Vighetto, 1988; Pohl, 1973; Ungerleider & Brody, 1977). These and similar findings suggest that the dorsal pathway plays a critical role in computing the visuomotor requirements of actions. That is, using the available visual inputs to guide the motor output. This is because such computations rely fundamentally on the ability to precisely locate candidates for action in space (where an object is), and precise judgements of object dimensions (how it can be acted upon; Goodale & Milner, 1992).

Behavioural research provides compelling evidence that the dorsal pathway in selectively recruited for processing of visual objects near hands. Specifically, there is associated enhancement in magnocellular processing and attenuation of parvocellular processing for visual objects that appear within perihand space. For example, Gozli and associates (2012) demonstrated that hand proximity enhances high temporal contrast of magnocellular neurons (sensitivity to object offsets/onsets) when using temporal and spatial gap tasks designed to selectively recruit the magnocellular and parvocellular networks respectively (Carey, et al., 1996; Dufour & Touzalin, 2008; Goodhew, et al., 2013; Gozli, et al., 2012). The (magnocellular) temporal gap task required the observer to detect a rapid onset and offset or ‘flicker’ in the target (a circle with a small gap in one quadrant). In contrast, the (parvocellular) spatial task required participants to detect a constant gap in the same briefly presented stimulus. The authors found greater visual sensitivity (\(d'\)) in the temporal gap task in conditions when the observer’s hands were directly next-to versus distant from the monitor and the reverse for the spatial task. These findings are consistent with both enhanced magnocellular and diminished parvocellular processing near the hand (Gozli, et al., 2012).

In addition to demonstrable changes in visual sensitivity near hands, further neurophysiological and behavioural findings provide evidence for perihand biases in the distribution and shifts of visuospatial attention. At the most basic level, behavioural research has shown that hand proximity biases figure ground assignment (Cosman & Vecera, 2010). That is, figures are more often assigned as foreground objects when presented near hands compared with figures presented near other non-hand visual anchors (Cosman & Vecera, 2010). The same research has shown that the biasing effects of hand position also competes with image-based information (such as concavity or convexity) to bias figure-ground assignment. Near-hand figures are assigned as foreground objects even when they included intrinsic concave cues. These findings suggest that hand proximity biases attention to objects that appear on the corresponding plane as the hand.
Supplementary to this, behavioural research suggests that hand location also biases the overall distribution of visuopsatial attention, such that near-hand targets capture spatial attention faster than those near the body but distant from hands. Reed and colleagues (2006) investigated the impact of hand proximity on covert shifts of visuospatial attention using predictive exogenous cues in a detection task in which onset targets appeared in the space either adjacent to or distant from the observers’ left or right hand. The authors found that target detection was faster for hand-adjacent versus -distant locations, irrespective of cue validity. This indicates faster engagement of visual attention to locations near versus distant from the hand, unaffected by highly predictive cues. In addition, when hands were occluded from view and next to the monitor, participants exhibited the same hand location visuospatial attention biases, which suggests that vision of the hands themselves was not required (Reed et al., 2006). Attentional bias towards a specific target location was extinguished when participants completed the task with a non-visual anchor or rubber hand in place of their real hand suggesting that they were not merely due to the presence of an additive visual cue (Reed et al., 2006). This combination of hand-side attentional biases for both visible and non-visible hands provides evidence that proprioceptive representation of the hand’s location contributes to near-hand visual perception.

Importantly, changes in the distribution and shifts of spatial attention are not restricted to visual inputs. For example, auditory localisation and the detection of objects in blind space are improved when objects are proximal to hands (Whitwell, Striemer, Nicolle, & Goodale, 2011). For example, Tseng and colleagues (2014) found that participants were faster to indicate the location (but not discriminate the pitch) of auditory stimuli when speakers were in near-hand space compared with the space distant from the hand. Similarly, evidence from single cell recordings in non-human primates suggests that there is greater neuronal firing within premotor cortex to auditory inputs, when they occur in near-hand space (Graziano, Reiss, & Gross, 1999). Moreover, Brown and colleagues (2008) found that size discrimination improved for visual objects in the blind hemifield of patients with geniculo-striatal lesions when a hand was adjacent to the object. Importantly, the observer’s ability to scale grip to pick up a target object successfully was preserved following damage to the magnocellular pathway. These findings suggest that hand proximity improves processing of object properties even in contexts where visual inputs are either absent or are unable to be processed. This in turn may indicate that attentional biases are driven by overlapping multisensory representations of the limb, supported by research which has shown that multisensory representation of the space near the body...
facilitates shifts in attention in the absence of visual inputs (Eimer, 2001; Macaluso & Driver, 2001; Santangelo, Van der Lubbe, Belardinelli, & Postma, 2006). That is, visual inputs are not necessary to facilitate near-body spatial attention shifts, or biases in attention distribution.

Critically, neurophysiological evidence suggests that shifts and biases in selective attention serve to enhance the perceptual processing of objects near the hand. Electrophysiological recordings have shown that there is attenuated P2 (a visual evoked potential typically associated with enhancements in cognitive processing (Hackley, Woldorff, & Hillyard, 1990; Noldy, Stelmack, & Campbell, 1990)) for objects which appear near the hand (Qian, Al-Aidroos, West, Abrams & Pratt, 2012). Importantly, this only occurred in contexts when individuals were directing attention to the near hand location, and not when they were attending to locations distant from the hand. These findings indicate that the combination of hand proximity and endogenous attention enhances later stages of perceptual processing.

Further electrophysiological research has directly shown that spatial attention plays a critical role in dorsal visual processing. For example, electrophysiological and functional imaging work has shown activation in regions of parietal cortex responsible for the spatial allocation of attention which modulates the dorsal visual stream (Goodale, 1990; Milner, et al., 2003; Milner, Harvey, & Pritchard, 1998). It is possible that lower level magnocellular biases in near hand processing are facilitated or driven by these multisensory biases in attention distribution. Shifts of visuo-spatial attention have previously been shown to facilitate visual sensitivity at the site of the attention shift, under a number of circumstances (Balz & Hock, 1997; Posner, 1980; Posner & Cohen, 1984; Yeshurun & Carrasco, 1998). Yet, to date the magnocellular enhancement account has failed to account for the contribution of body centred biases in spatial attention to enhancements found near-hand visual perception.

The aim of the present research was to examine the directionality of the relationship between covert endogenous attention and near hand magnocellular sensitivity enhancements. Near-hand visual enhancements may be the result of the greater allocation of endogenous visuo-spatial attention which enhances magnocellular sensitivity, or alternatively increased magnocellular sensitivity may drive shifts in endogenous visuo-spatial attention. To examine this, we investigated two magnocellular properties: onset detection (operationalised as luminance contrast sensitivity) and object size discrimination (operationalised as aspect ratio discrimination sensitivity). These two types of visual processing were of interest because on the role they play in guiding manual
actions. Onset detection is crucial for localising candidates for action and contributes to the planning of reach trajectories by guiding the direction and distance of the reach. Importantly, processing of such inputs occurs in the magnocellular visual pathway early in visual perception. For example, visual contrast sensitivity arises in midget cells in the retina, prior to conduction through to the magnocellular layers of LGN and through to the dorsal visual stream (Goodale & Milner, 1992; Kaplan & Shapley, 1986). This enabled us to examine how selective visuospatial attention contributes to the perception of early visual inputs.

By contrast, object dimension judgements require higher order discriminations of an object’s visual properties, and occur later in the course of visual processing. For manual action, the ability to judge the size and dimensions of a candidate target for action is important for guiding sensorimotor transformations such as scaling of the digits to successfully grasp an object. Thus size discrimination requires precise representation of the relative dimensions of an object’s component parts because this is critical for judging axes of symmetry (Brown, et al., 2008; Derrington & Lennie, 1984; Legge, 1978).

Typically, basic judgments of objects dimensions are subject to the classic V-H illusion, whereby the vertical dimensions of objects are over-judged relative to the horizontal dimensions. That is, objects are perceived to be taller than they are wide when both dimensions are the same objective length (Künnapas, 1955; Künnapas, 1957). We employed an aspect ratio task which exploited the properties of the Vertical-Horizontal (V-H) Illusion to investigate how hand proximity influences object dimension judgements. Yet, reaching to grasp movements are relatively immune to such illusions (Aglioti, DeSouza, & Goodale, 1995; Milner, Goodale, & Vingrys, 2006; Vishton, Rea, Cutting, & Nuñez, 1999). The ability to scale successfully one’s digits based on the dimensions of an object does not reflect an over-judgment of the vertical dimensions of the object. Observers are able to scale their digits in a way which reflects accurately the dimensions of the object being reached towards. These findings indicate that visual object perception is shaped by how or whether we plan to act on an object (Aglioti, et al., 1995). Further, they suggest that V-H Illusion results when there is selective recruitment of the ventral visual pathway and not when visual inputs are selectively processed in the dorsal pathway. If hand proximity is sufficient to facilitate dorsal engagement, objects near hands should benefit from selective recruitment of the dorsal pathway and the V-H illusion should be attenuated relative to when objects are distant from the hands.

Reed and colleagues (2006) have shown that perihand space is covertly monitored in attention, and as a result endogenous attention shifts faster to objects which onset near
hands compared with those distant. We postulated that this endogenous attentional advantage would enhance near hand visual sensitivity for onset detection and for dimension judgements (as opposed to the inverse relationship). To this end, we modulated the extent of covert endogenous attention shift possible prior to target offset by presenting targets (squares of varying luminance contrasts for Experiment 1, and rectangles of varying aspect ratios for Experiment 2) for a duration of either 43ms or 250ms. Neurophysiological and behavioural evidence has shown that endogenous shifts of visuospatial attention occur after around 200ms following stimulus presentation (Goldberg & Segraves, 1987; Harter, Miller, Price, LaLonde & Keyes, 1989). As a result, targets which onset for the 43ms duration would offset prior to shifts in endogenous attention. By contrast, for the longer stimulus duration (250ms), endogenous shifts could be completed prior to target onset and in turn may facilitate processing of object properties. The employment of a 43ms presentation time in the shorter instance should not negate the observer’s ability to shift exogenous visuospatial attention to the target (which previous work by Klein and Dick, 2002) shows can occur as early as 15ms following target onset) but instead should not enable the observer’s ability to shift endogenous attention prior to object offset. Thus objects which appear for < 200ms should not benefit from higher order cognitive processing that engagement of endogenous attention incites (Hackley et al., 1981; Qian et al., 2012). Targets remained un-masked to allow evaluation of any after-image attention shifts for both short and long stimulus durations. Targets were also reliably presented in a consistent location to either the left or right of fixation, to enable observers to covertly monitor discrete locations on the display.

**Experiment 1**

Lesions in the magnocellular layers of LGN of non-human primates result in deficits in contrast sensitivity particularly for low spatial and high temporal frequency inputs (Maunsell, et al., 1990; Maunsell, et al., 1999; Merigan & Maunsell, 1990). This direct link between contrast sensitivity (the ability to distinguish an object from its background (Enroth-Cugell & Robson, 1966), and magnocellular activity means that contrast sensitivity provides a clear psychophysical measure of magnocellular recruitment (Legge, 1978; Merigan & Maunsell, 1990). Thus, measuring contrast sensitivity is one of the most effective means for isolating magnocellular from parvocellular activity (Legge, 1978). Studies of near-hand visual perception have exploited these properties to investigate the comparative recruitment of magnocellular and parvocellular pathways to process near-hand inputs (Davoli, et al., 2010; Goodhew, et al., 2014; Goodhew, et al., 2013; Gozli, et
al., 2012; Tseng & Bridgeman, 2011). In the first experiment, we tested one of the most basic measures of contrast sensitivity – sensitivity to detection of objects of varying luminance intensities, to investigate how hand proximity and ability to shift visuospatial attention modulates visual sensitivity.

Earlier findings suggest that attention modulates visual sensitivity for specific object properties near hands. In particular, Dufour and Touzalin (2008) found greater accuracy and faster response times when observers detected the illumination of LED targets (presented for 500ms) presented near versus distant from one of the participants hands. These behavioural findings suggest, consistent with the magnocellular enhancement account, that there is greater visual sensitivity for luminance contrasts which onset near hands (reflected in greater accuracy for detecting targets of lower luminance intensities within the perihand zone). Yet, because targets were presented for an extended period of time (>250ms), improved visual sensitivity in the perihand zone may have also benefitted from enhanced shifts of visuospatial attention to the hands location (relative to those towards locations that did not contain the hand). This is an important consideration because it suggests that the allocation of visuospatial attention may be driving enhanced magnocellular near-hand perception. Thus, in the first experiment we aimed to disambiguate effects of attention from this finding, by examining whether visual sensitivity to luminance contrasts occurs for stimuli presented too briefly to benefit from covert shifts of attention to the hands location. Specifically we aimed to establish, whether near hand magnocellular enhancements are driven by bottom-up biases in visuospatial attention as opposed to sharpened visual receptive for near-hand multisensory neurons or other hand-centred visual processes.

In Experiment 1 we used a method of constant stimuli with a luminance contrast manipulation and compared performance on a left-right detection task completed with hands adjacent to or distant from the display. Observers indicated the onset of the target by responding with the hand-aligned to the target side (left-hand for left-sided targets, right–hand for right sided targets) and targets were presented for either 43ms or 250ms. The short target presentation of 43ms was designed to elicit maximal magnocellular activation (due to the brief onset/ offset of the stimuli), but not to enable a shift in covert visuospatial attention prior to target offset. The longer stimulus presentation of 250ms was utilised to enable shift in attention to the target location prior to offset. Luminance targets were either sub-threshold, low contrast, or high contrast relative to the display background. Based on previous findings that near-hand contrast sensitivity biases are driven by magnocellular enhancements which occur early is visual perception, we tested the
competing predictions. If underlying biases in visuospatial attention do not contribute to magnocellular enhancements for object detection, there should be greater visual sensitivity (reflected by a lower detection threshold and greater accuracy of target detection) for hands-adjacent versus hand distant postures irrespective of target duration. Conversely, if visuospatial attention drives or contributes to near-hand magnocellular enhancements, greater visual sensitivity for near versus distant hand postures should only be evident for the long stimulus duration (250ms) and not for brief stimulus presentation.

**Method**

**Participants.** The same twelve participants (8 females, mean age = 24.36), completed Experiments 1 and 2 (the order of experiment and task completion was randomised). All were right-handed by self-report with normal or corrected-to-normal visual acuity.

**Stimuli and Apparatus.** The task was conducted on a PC computer (Intel Pentium 4 processor) and a CRT monitor (refresh rate of 60Hz) using Matlab and Cogent toolbox. Responses were recorded using standard QWERTY keyboards that were mounted to the sides of the monitor (with the response button directly horizontally aligned with the target stimuli and fixation for the hands-near conditions) and directly in front of the monitor (for the hands-distant condition). Response buttons were 10cms from the target location on their comparative side in the hands-near conditions or on the desk aligned 25cms directly in front (towards the participant) of the front plane of the monitor in the hands-distant condition (see Figure 1 for representation of set up). Stimuli were presented on a white background (66cd/m²). The target in each trial was a 1cm square (1.5° visual angle) which varied randomly in luminance from the following levels; 60.4, 61.5, 63.4, 65, 66 (note: this was the same as the background and served as the baseline stimulus), 67, 68.4, 69.2, 70.7 cd/m². Sub-threshold stimuli were those within 1 cd/m² of the background luminance (65 and 67 cd/m²), low contrast were those 2-3 cd/m² of the background luminance (63.4 and 68.4 cd/m²), high contrast were those within 4-6 cd/m² of the background luminance (60.4, 61.5, 69.2 and 70.7cd/m²) Targets could appear with equal probability to either the left or right of fixation.
**Procedure.** Participants were seated in a quiet, dimly-lit room with their head restrained in a chin rest 40cms from the monitor. Presentation of a fixation cross (1.5° visual angle) initiated each trial. The fixation cross remained onscreen for the duration of the trial. Following a pre-trial-period which varied randomly from 800 – 2000ms, a target appeared for either 43ms or 250ms to either the left or right of fixation (location randomised within blocks) and the participant was required to indicate on which side of the screen the target appeared. The fixation point extinguished 250ms following the presentation of the target stimulus.

Hand position was blocked: hands-adjacent and hands-distant. In both block types participants were instructed to respond with the hand that was aligned with the stimulus – left hand for targets appearing in the left hemifield and right hand for targets appearing in the right hemifield. In the hands-adjacent block, participants responded to the target by pressing the allocated left or right response keys on the keyboards mounted to the left and right of the CRT monitor screen respectively. In the hands-distant blocks, participants responded to the target by pressing the allocated left or right response key (left control and right control respectively) on the keyboard that was distant from the monitor. Participants completed the task in blocks of 90 trials, three repetitions of each block type (with block order randomised between participants) resulting in a total of six blocks and 540 trials in total.

**Results and discussion**

**Accuracy.** To analyse the impact of hand proximity, we conducted a two condition (hands-near; hands-distant) by nine luminance (60.4, 61.5, 63.4, 65, 66, 67, 68.4, 69.2, 70.7 cd/m²) repeated measures analysis of variance (ANOVA) on the proportion of correct responses for each of the stimulus presentations (43ms and 250ms). Following this we also a combined analysis to investigate the impact of target duration.
Table 1. Means, with standard error in parenthesis, t-statistics, and p-values for comparisons to the control luminance intensity (66 cd/m²), for Experiment 1.

<table>
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<tr>
<th>Luminance (cd/m²)</th>
<th>Mean (SE)</th>
<th>t-statistic</th>
<th>p – value</th>
<th>Effect size (d)</th>
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<td>.87 (.03)</td>
<td>9.97</td>
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43ms. We followed up a significant main effect of luminance intensity $F(8, 88) = 36.20, p < .015, \eta^2_p = .77$ by comparing each level of luminance to the control level (66 – same luminance as background) to the control condition (zero deviation from background luminance). Participants displayed greater accuracy for detecting all luminance contrasts relative to the control except those closest to the background luminance 65 and 67 cd/m²; (see table 1 for means and comparison statistics).

250ms. The only significant finding was a main effect of luminance contrast $F(8, 88) = 50.86, p < .001, \eta^2_p = .82$. Accuracy of target detection was significantly better for all stimulus contrasts relative to the control (see table 1 for means and comparison statistics). An analysis which compared participant’s responses on the control condition to chance (.50) revealed that when the object was the same luminance as the background, participants were significantly worse than chance at identifying the target location. This was not the case for the shorter target presentation time (43ms: $M = .48, SE = .05, t(11) = .47, p = .647$, 250ms: $M = .36, SE = .05, t(11) = 2.67, p = .022$).

43ms and 250ms comparison. There was an interaction between target duration and luminance contrast $F(8, 88) = 6.11, p < .001, \eta^2_p = .35$. Follow-up pairwise comparisons were conducted between the 43ms and 250ms target durations for each level of luminance intensity. For low frequency contrasts (63.2 and 68.4 cd/m²) accuracy was greater when the target was presented for 250ms versus 43ms ($t(11) = 4.15 p = .002$ and
Importantly, for the high luminance contrasts (those most removed from the background luminance; 60.4 and 70.7 cd/m²) the reverse was true, accuracy was better for detecting targets presented for 43ms versus 250ms (t(11) = 3.87, p = .003, d = .76 and t(11) = 2.92, p = .014, d = .66 respectively; 60.4 cd/m² 43ms: M = .97, SD = .03, 250ms: M = .89, SD = .09; 70.7 cd/m², 43ms: M = .97, SD = .04, 250ms: M = .87, SD = .12 – see Figure 2).

Figure 2. Graphical representation of the interaction between target duration and luminance intensity for proportion of correct responses (** p < .005, * p < .05), error bars depict standard error.

Thus for low contrast targets, target detection accuracy improved for longer onsets compared with brief onsets. By comparison, for high contrast targets, target detection accuracy improved for brief onsets compared with longer onsets. These findings suggest that, consistent with magnocellular stimulus properties, high contrast stimuli are detected optimally when presented briefly compared with for longer durations (Denison & Silver, 2012; Derrington & Lennie, 1984). They also indicate, in line with earlier findings, that visuospatial attention facilitates detection of low contrast luminance onsets (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Reynolds, Pasternak, & Desimone, 2000). One surprising finding was the worse than chance detection performance for the 250ms presentation of the control luminance. This may reflect a response bias that arises in contexts of perceptual uncertainty (e.g. bias to respond with the dominant hand) that were specific to the longer stimulus duration. For example, they may reflect that shifts of
visuospatial attention across what is effectively an empty display over a longer duration of time, may result in participant exhibiting a response biases (such as a dominant hand bias) to respond in such contexts, that does not occur for more brief stimulus presentations. Taken together, these results allow us to conclude that we successfully recruited the magnocellular visual stream, but there was no evident impact of hand location on the accuracy of visual onset detection for the target durations used.

**Visual sensitivity.** To evaluate the impact of hand proximity on visual thresholds, we calculated the point of subjective equality (PSE - sigma) of the Gaussian function for each target duration and hand posture, and stimulus presentation duration. For the 43ms target duration, a comparison of PSEs between the hands-adjacent ($M = 2.35$, $SD = .64$) and hands-distant ($M = 2.37$, $SD = .61$) conditions, found no significant difference in visual sensitivity for luminance onsets $t(11) = .19$, $p = .85$ n.s. There was also no significant difference in visual sensitivity for the 250ms comparisons between the hands near ($M = 2.43$ $SD = .79$) and hands far condition ($M = 2.60$, $SD = .90$) $t(11) = .97$, $p = .354$ n.s.

Comparing between the 43ms and 250ms target durations for each hand posture similarly revealed no differences between visual sensitivity relative to target presentation duration for the hand-near or hands-distant posture $t(11) = .37$, $p = .722$ and $t(11) = .80$, $p = .441$ respectively. These findings indicate that visual sensitivity did not improve relative to the location of the hands, irrespective of target duration.

Taken together, the above results indicate that there was demonstrable impact of hand proximity on either the accuracy of luminance onset detection or contrast sensitivity. That is, we found no evidence that hand proximity either facilitated or impaired luminance contrast sensitivity for targets presented for < 250ms. When considered in combination with the results of Dufour and Touzalin (2008), the current findings suggest that when stimuli were presented for 250ms or less, greater visual sensitivity is not apparent for luminance onsets near versus distant from the hand. By contrast, Dufour and Touzalin (2008) found that visual sensitivity improved near the hand for luminance onsets which were presented for longer stimulus durations (500ms). This suggests that near-hand magnocellular facilitation may occur later, perhaps as the result of top-down allocation of attention.

Further, there was an absence of perceptual facilitation for even the longer stimulus durations relative to hand proximity. Shifts in spatial attention to the hands location occur at around 200ms, thus it may be the case that visual sensitivity for low contrast targets near the hands, occur only when targets are presented for longer than 250ms. This is somewhat counter to the magnocellular enhancement account which proposes that
detection for rapid onsets/ offsets should be facilitated for objects near hands. Instead, results suggest that for threshold stimuli there is no measurable benefit attributable to hand proximity. That is, there is no additive benefit to one’s ability to discriminate a low threshold stimulus from its background, even for briefly presented stimuli.

The most robust finding from Experiment 1 was greater contrast detection accuracy relative to shifts of visuospatial attention. We found improved perception for low contrast stimuli for longer stimulus presentations, and improved perception for high contrast stimuli for brief presentations. These findings fit in with properties of magnocellular neurons and indicate further specialisation in the visual system to process action relevant stimulus inputs (Denison & Silver, 2012). Visuospatial attention facilitates distinguishing an object from its background, so in the context of high contrast stimuli, shifts of visuospatial attention are not required to facilitate target detection. This suggests that onset detection is driven by bottom-up visual (magnocellular detection). For low contrast stimuli, however, the results suggest that shifts in visuospatial attention to the target location improve contrast sensitivity. This in turn indicates that perceptual processing of low contrast luminance onsets is driven by top-down allocation of visuospatial attention.

Thus when considered in the context of previous research, the results of Experiment 1 provide further evidence that shifts in visuospatial attention enhance contrast sensitivity. Moreover, near-hand magnocellular enhancements may occur as a result of top-down attentional facilitation of action-relevant inputs, and such shifts occur later in the processing of visual inputs (after 250ms). These findings indicate that enhancements in magnocellular processing for low contrast stimuli are driven by shifts in visuospatial attention.

**Experiment 2**

In the second experiment, we investigated whether biases in visuospatial attention improve the precision of object dimension judgements in near-hand space. Current understanding of the magnocellular visual pathway is that it is involved in the mediation of visuomotor transformations required for visually guided action (see Goodale & Milner, 1992 for review). The ability to judge the size and dimensions of visual objects is fundamental to developing the kinematic properties of actions towards that object. This includes grip scaling which relies fundamentally on judgements of the axes of symmetry (the locations on an object that must be grasped in order to successfully pick up an object) (Carey, et al., 1996; Vishton, et al., 1999; Whitwell, et al., 2011). Neuropsychological evidence indicates that the allocation of spatial attention to a given object is critical to
one’s ability to judge such object dimensions. This is evident in studies of unilateral spatial neglect patients. These showed that when objects were presented in the neglected visual field, patients misjudged the size of the object and were unable to scale their digits appropriately to facilitate a successful grasp (Milner, et al., 1998). Such impairments result from damage in the parietal regions of the dorsal visual stream; areas within premotor cortex, which are involved in directing top-down attentional resources to space near the body and which enhance processing of action-relevant visual inputs (Rizzolatti & Berti, 1990; Stein, 1992). It is possible that goal-directed shifts of visuospatial attention facilitate action specific object processing and in-turn enhance magnocellular perception in near-body space. Specifically, attention engages the dorsal (versus ventral) stream to process the dimensions of actable objects.

To investigate whether this is the case we used the V-H Illusion to examine and how hand proximity and visuospatial attention contribute to the precision of object dimension judgements. Extending on previous research, we aimed to evaluate whether only hand proximity was sufficient to engage dorsal processing of near hand objects, and thus reduce the observer’s susceptibility to the V-H illusion. The secondary aim of Experiment 2 was to examine the role that visuospatial attention plays in such near-hand object judgements. That is, whether changes found by studies of prehension reflect an underlying change to near-hand visual object perception, changes to the way that visuospatial attention is directed towards near hand objects, or a combination of both. To do this, we evaluated whether reductions in the illusion occur at the early levels of visual perception or when visual objects benefit from shifts in visuospatial attention to the hand location. We utilised an aspect ratio task which required observers to judge in which dimension (width or height) a variably sized target rectangle was largest. The task required observers to compare both the vertical and horizontal dimensions of an object prior to making the judgement. When hands were adjacent to the visual display, we predicted that there would be greater visual sensitivity for object dimension judgements, as indicated by a reduced V-H illusion and lower response bias threshold. We also predicted that this would occur for longer (250ms) but not shorter stimulus presentations (43ms) due to the more higher-order nature of such judgements compared with more basic target detection.

Method

Stimuli and apparatus. These were the same as for Experiment 1 with the exception that target in each trial was a rectangle which varied randomly in width to height ratio from 50:49, 25:24, 50:47, 25:23, 1:1, 49:50, 24:25, 47:50, 23:25 and could appear
with equal probability to either the left or right of fixation. Targets also varied randomly in size from 30 – 110 pixels to prevent participants using size cues from the stimuli to infer aspect ratio.

Design and procedure. Procedure was the same as for Experiment 1 with the exception of the following. Participants responded to the targets by indicating in which dimension (width or height) the rectangle was largest. Participants responded with the hand aligned with the target (left hand for left hemiﬁeld target/ right hand for right-hemiﬁeld targets) and pressed the response button in the upper location if the rectangle was taller and the button in the lower location if it was wider. This response alignment was utilised to avoid added error variance from stimulus-response compatibility effects (Proctor & Reeve, 1990). In the hands-near condition responses were made on the keyboard mounted to the left and right of the monitor, in the hands-distant condition responses were made on the keyboard mounted distant from the monitor. Participants completed a block of the task in which the target was presented for 43ms and one where it was presented for 250ms.

Results and discussion

Responses on the task were coded relative to whether participants made a taller or wider response to the object. Wider responses were coded as 0 and taller responses coded as 1 then responses were averaged over levels of aspect ratio and condition for each participant. A response value of .50 reﬂects equal probability of indicating the object is taller or wider. Responses > .5 are indicate that more ‘taller’ versus ‘wider’ responses were made (the participant perceived the object to be larger in the vertical dimension) and those < .50 indicate that more ‘wider’ versus ‘taller’ responses were made (the participant perceived the object to be larger in the horizontal dimension).

For each of the hand posture and target duration conditions, the proportion of taller to wider responses was compared to the equal probability of making a taller versus wider response to a square stimulus to evaluate in which conditions the V-H Illusion occurred. For both of hands far conditions, participants signiﬁcantly overestimated the vertical dimension (43ms: $M = .62, SE = .03, t (11) = 3.47, p = .005, d = .72$, 250ms: $M = .69, SE = .05, t (11) = 4.24, p = .001, d = .79$). For both of the hands near conditions, there was no signiﬁcant difference between the proportion of taller to wider responses and the equal probability of making a taller versus wider response when correcting for multiple comparisons $p > .012$ (43ms: $M = .57, SE = .06, t (11) = 1.34, p = .207, d = .37$, 250ms: $M = .63, SE = .05, t (11) = 2.93, p = .014, d = .66$). These ﬁndings suggest that there was a
V-H Illusion for the square stimulus when hands were distant from the display, but not when hands were next to the display.

**Response accuracy.** A two condition (hands-near; hands-distant) by nine aspect ratio (50:49, 25:24, 50:47, 25:23, 1:1, 49:50, 24:25, 47:50, 23:25) repeated measures analysis of variance was conducted on the response averages. Separate ANOVAs were conducted on the proportion of taller to wider responses for each of the target durations (43ms and 250ms) to establish whether hand proximity impacted these differentially relative to stimulus duration (and thus the observers ability to shift endogenous attention). Following this, the proportion of taller to wider responses was compared between target durations for each hand posture, with an additional ANOVA to establish whether the observers ability to shift endogenous visuospatial attention to the target location, impacted on their ability to perceive the dimensions of the target object.

Table 2. Means, standard errors and statistics for comparisons to standard stimulus.

<table>
<thead>
<tr>
<th>Aspect ratio (W:H)</th>
<th>Mean (SE)</th>
<th>43ms</th>
<th>250ms</th>
<th>t-statistic</th>
<th>43ms</th>
<th>250ms</th>
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<td>.20(.04)</td>
<td>9.15</td>
<td>7.91</td>
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<td>&lt;.001</td>
<td>.94</td>
<td>.92</td>
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<tr>
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<td>&lt;.001</td>
<td>.84</td>
<td>.91</td>
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<tr>
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<td>&lt;.001</td>
<td>&lt;.001</td>
<td>.84</td>
<td>.94</td>
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<tr>
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<td>3.45</td>
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<td>.91(.02)</td>
<td>8.06</td>
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<td>&lt;.001</td>
<td>&lt;.001</td>
<td>.92</td>
<td>.90</td>
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**43ms.** The only significant finding was a main effect of aspect ratio $F(1,6) = 71.37, p < .001, \eta_p^2 = .87$. We followed this up by comparing each level of aspect ratio to the baseline ratio (1:1). For the stimuli that were wider (50:49, 25:24, 50:47, 25:23) participants made significantly fewer ‘taller’ responses compared with the baseline stimulus. For all stimulus levels that were taller (49:50, 24:25, 47:50, 23:25), participants made significantly more ‘taller’ responses compared with the baseline stimulus (see Table
2 for means and summaries of comparisons and Figure 3a for graphical representation). No other main effects of interactions reached significance.

![Figure 3](image)

**Figure 3.** ‘Taller’ responses relative to hand posture, aspect ratio and target duration. Figure 3a) represents the relationship between hand posture and aspect ratio for the 43ms duration and Figure 3b) represents the relationship between hand posture and aspect ratio for the 250ms duration. For aspect ratio 1 = 50:49, 2 = 25:24, 3 = 50:47, 4 = 25:23, 5 = 1:1, 6 = 49:50, 7 = 24:25, 8 = 47:50 and 9 = 23:25. * p < .05.

250ms. There was a main effect of aspect ratio $F(8,72) = 87.23, p < .001, \eta^2_p = .89$. We followed this up by comparing each level to the adjoining aspect ratio value. We found that for the stimulus levels that were wider than they were tall (50:49, 25:24, 50:47, 25:23) participants had significantly fewer ‘taller’ responses compared with the baseline stimulus. For stimulus levels that were taller than they were wide (49:50, 24:25, 47:50, 23:25), participants made significantly more ‘taller’ responses compared with the baseline (see Table 2 for means and t-statistics and Figure 3b for graphical representation).

There was also an interaction between aspect ratio and hand posture $F(8,88) = 2.76, p = .009, \eta^2_p = .20)$. Follow-up paired samples t-tests compared each aspect ratio between hands conditions. This revealed that participants made significantly fewer ‘taller’ responses in the hands-near condition versus hands-distant condition, for stimulus closest to square that was wider than they were tall 25:23 ($t(11) = 2.74, p = .019, d = .64$). This finding suggests, consistent with prediction, the vertical-horizontal illusion was reduced for near hand objects presented for 250ms.
Figure 4. ‘Taller’ responses where 1 = all ‘tall’ responses and 0 = all ‘wider’ responses for the hands near posture by aspect ratio (1 = 50:49, 2 = 25:24, 3 = 50:47, 4 = 25:23, 5 = 1:1, 6 = 49:50, 7 = 24:25, 8 = 47:50 and 9 = 23:25) and target duration ** p < .001.

Comparison between 43ms and 250ms. There was a significant interaction between hand posture and aspect ratio $F(8,88) = 2.76, p = .013$, $\eta^2_p = .19$. Across stimulus presentation times, participants made more ‘wider’ responses for the 25:24 aspect ratio, when hands were near versus distant from the monitor $t(11) = 4.24, p = .00$, $d = .79$. This finding suggests that, overall there was a reduction in the vertical-horizontal illusion when stimuli were presented near versus distant from hands.

Visual sensitivity. The primary measure of interest was whether hand proximity influenced the observer’s sensitivity to changes in object dimensions. To evaluate this we fit a cumulative Gaussian to the proportion of taller to wider responses for each aspect ratio relative to hand location and target duration. This provided us with a measure of the point of subjective equality (PSE - sigma) for each hand posture and target duration for each participant. Comparisons of PSEs for the 43ms stimulus presentation revealed a trending difference in visual sensitivity for aspect ratio judgements between the hands near ($M = 4.52, SD = 1.25$) and hands far conditions ($M = 5.56, SD = 2.47$), $t(11) = .43, p = .090$, $d = .55$, however this did not reach statistical significance. Comparisons of PSEs for the 250ms stimulus presentation found that the threshold for the hands near condition ($M = 3.10, SD = 1.20$) was significantly lower than for the hands far condition ($M = 3.98, SD = 1.90$), $t(11) = 2.90, p = .015$, $d = .57$. This suggests, consistent with the predicted relationship, that observers had greater visual sensitivity (smaller point of subjective equality) when judging the dimensions of objects near versus distant from hands.
Comparison of PSEs between the 43ms and 250ms stimulus presentations revealed that for the hands-near condition, there was significantly greater visual sensitivity when targets were presented for 250ms ($M = 3.10$, $SD = 1.20$) versus 43ms ($M = 4.52$, $SD = 1.25$) $t(11) = 3.38$, $p = .006$, $d = .94$. This provides evidence that shifts of visuospatial attention to the target location, improved visual sensitivity for aspect ratio judgements.

Figure 5. Visual thresholds (sigma) for ‘taller’ responses by target duration and hand proximity. ** $p < .010$

Experiment 2 presents two novel findings, the first of which is that there is a reduction in the visual-horizontal illusion for near-hand stimuli. This finding is important because it indicates that the accuracy of size judgements are improved for visual objects, even when the actor is not planning to actively grasp it. That is, mere hand proximity improves the accuracy of visual perception for grasp-relevant object properties. The second element of this finding was that reduction of the V-H illusion was only evident for the longer stimulus presentation time (250ms versus 43ms). This provides further evidence for attention driven changes to visual perception based on the actable properties of an object. Moreover, this finding provides evidence that mere proximity of the hand facilitates shifts of attention which in turn further improves the accuracy of object dimension judgements.

The second finding in Experiment 2 was greater visual sensitivity for object dimension judgements when hands were adjacent to the display for the longer stimulus presentation duration. This enhancement in visual sensitivity was relative both to the proximity of the hands, and to the duration of stimulus presentation. This was such that enhanced visual sensitivity were only observed for near hand conditions for longer
stimulus durations. This is a critical finding because it suggests that for neuro-typical observers, visuospatial attention must be shifted to the objects location to enhance processing of action relevant inputs (improve perception of object dimensions). Enhancements do not occur when objects are presented too briefly to benefit from shifts of visuospatial attention.

**General Discussion**

The present study investigated how shifts in visuospatial attention impact near-hand magnocellular visual processing. This was motivated by neuropsychological evidence that impairments in the ability to shift visuospatial attention results in corresponding impairments in perceptual processing of near-hand objects (Aglioti, et al., 1995; Milner, et al., 1998). Primarily, we were interested in whether perceptual processing of the magnocellular properties, critical for the planning of manual actions, was enhanced when shifts of visuospatial attention could be completed during target presentation. We examined two elements of magnocellular processing relevant to manual action: luminance onset detection (Experiment 1) and object dimension judgments (Experiment 2) and investigated how hand proximity and ability to shift visuospatial attention to the visual object prior to offset impacted the visual accuracy and sensitivity of object judgements.

With regards to luminance onsets, the results showed that shifts of visuospatial attention but not hand proximity improved accuracy of onset detection for low contrast targets. Conversely, brief presentation of stimuli improved the accuracy of onset detection for high contrast targets. We found that contrary to earlier findings (Dufour & Touzalin, 2008), there was no evidence of enhancements in luminance contrast sensitivity when hands were adjacent to compared with distant from the display. Despite the demonstrated enhancements in temporal shifts in attention for high/contrast onsets and offsets near hands found by others, hand proximity for stimulus presentation < 250ms did not improve spatial shifts to such basic magnocellular inputs.

The present findings may suggest that briefly presented stimuli do not appear for long enough to represent candidates for action and subsequently drive shifts in spatial attention. This is particularly likely in light of findings from Dufour and Touzalin (2008) that for longer stimulus presentations (+500ms), contrast sensitivity was enhanced near hands. Thus, the current pattern of results may reflect that in guiding the sensorimotor transformations required to interact with a target, brief onsets/offsets of high and low contrast stimuli do not elicit shifts in spatial attention. Consequently, this may indicate that the mechanisms driving previously demonstrated enhancements in temporal processing
are at least in part dissociable from those responsible to driving shifts in spatial attention to near-hand objects (Abrams, et al., 2008; Goodhew, et al., 2014; Goodhew, et al., 2013; Gozli, Ardron, & Pratt, 2014; Gozli, et al., 2012). In turn, the current findings may also indicate that multisensory representation of the limb contributes substantially to spatial shifts in attention, but less so to temporal enhancements in magnocellular processing.

With regards to object dimension judgements we found that hand proximity improved visual sensitivity for object dimension judgments but only when targets were presented for the longer stimulus duration (250 ms). This provides evidence that visual perception benefited from shifts of attention to the target, as enhanced visual sensitivity is not evident for targets presented for the shorter duration (43ms). Taken together, the described findings indicate near-hands magnocellular enhancements occur relative to the type of stimulus property being judged and, importantly, relative to the observer’s ability to shift visuospatial attention to the target location prior to offset. This extends on earlier work because it demonstrates that there is enhanced perceptual processing of visual properties that are relevant to more complex elements of manual actions, such as grip scaling (as opposed to trajectory guidance which is impacted by target onsets/offsets) when objects are presented in mere proximity to the hands, but only following shifts of attention.

The most empirically interesting finding was that hand proximity both improved visual sensitivity and attenuated the V-H illusion for object dimension judgements. In other words, shifts in visuospatial attention improve the precision of object dimension judgements. Thus, consistent with the findings of Reed and colleagues (2006), hand location provides an important cue for spatial attention. Moreover, this support the theory that it is the allocation of additional attentional resources which in turn drives magnocellular enhancements in the perihand region.

Previous conceptualisations of the dorsal visual stream suggest that top-down modulations in visual processing occur relative to the goals of actions. The present findings in part support this supposition, because they indicate that task goals (to detect versus discriminate the size of an object) modifies the impact that hands have on visual processing. That is, perceptual processing of objects which require higher order judgements such as size discrimination, benefit more from additional attentional resources than do more baseline visual judgements such as onset detection. From this finding it appears that hand proximity is enough to drive changes in the distribution of visuospatial attention and in turn the precision of object dimension judgements. Unlike previous studies which examined visual size judgements in prehension, we found evidence that the observer need not grasp an object for attentional enhancement to occur.
In sum, with regards to visual detection, we found evidence that sharpened visual receptive fields for near body onsets cannot entirely account for the enhancements in onset detection found by others. We did not find evidence of facilitated onset detection when hands were proximal versus distal from the body. As a result of this, it would be of empirical benefit to identify the conditions under which hand proximity may facilitate luminance contrast sensitivity, as previous research suggests longer stimulus presentations may play a role in this process. Our findings contribute to understanding the mechanisms which underpin enhancements size discrimination for visual objects in near-hand space. In light of these findings it appears likely that increased allocation of visual attention within near-hand space, and not sharpened visual receptive fields for near hand stimuli are what drives enhancements in near-hand magnocellular visual processing.
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CHAPTER 3: HANDEDNESS AND GRASPABILITY MODIFY SHIFTS OF VISUOSPATIAL ATTENTION
In the first study I drew upon the two visual pathways theory (Goodale & Milner, 1992) to investigate how shifts of visuospatial attention impact near-hand visual enhancements. The results of Study 1 indicated that hand proximity enhanced the processing of magnocellular inputs relevant for grip scaling, when targets could benefit from shifts of endogenous visuospatial attention prior to target offset. These and earlier findings contribute to a body of evidence which illustrate that endogenous attention plays an important role in enhancing the perceptual processing of candidates for action. Specifically, they suggest that the presence of the hands near an object, enhances the engagement of endogenous attention. However, alternative research has also demonstrated that there are earlier reflexive biases in attention shifting near the body, which reflect a prioritisation of objects which onset near hands. Importantly, they have shown that the underlying functional properties of hands influences the speed of these reflexive (exogenous) attention shifts, such that they are faster to objects that are graspable or near the dominant hand (Le Bigot & Grosjean, 2012; Reed, et al., 2010; Roberts & Humphreys, 2011; Rubichi & Nicoletti, 2006).

Such reflexive attention biases may play a critical role in the later engagement of endogenous attention. Thus it is important to understand how they contribute to the overall distribution of visuospatial attention, to have a unified understanding of the role that attention plays in processing candidates for action. Critically, in addition to contributing to endogenous attentional processing, faster exogenous attention capture near hands may also facilitate the identification of new objects which may present obstacles to planned actions. That is, non-target objects near the hands may capture attention to allow the visuomotor system to adapt subsequent movement.

Importantly, earlier research suggests that such reflexive shifts are bounded to the functional properties of hands, consistent with the embodied theory of cognition. It is not just hand proximity but also the biomechanical grasping capabilities of different surfaces of the hand (such as the palm or back of hand) which contribute to these reflexive biases, and the continued presence of the hands near the target object may then serve to engage higher-order endogenous attention shifts (as we demonstrated in Study 1).

However, there are a number of issues with previous research, which makes it unclear how exactly differences in the intrinsic representation of hands impact exogenous attention. One of the most critical issues is that previous studies fail to concurrently account for the two primary intrinsic factors which impact the representation of hands; handedness and grasping capability. Both grasping affordances and handedness reflect intrinsic differences in limb representation, but which are underpinned by different neural
processes. With regards to handedness, they reflect structural and functional differences in the neural representation of dominant and non-dominant hands (Amunts et al., 1996; Fernandez & Bootsma, 2004; Nordin & Frankel, 2001; Schieber & Santello, 2004; Sörös et al., 1999; Volkmann, Schnitzler, Witte, & Freund, 1998). Conversely, grasping affordances reflect the biomechanical constraints of manual action (Castiello, 2005; Grafton et al., 1996). For example one can only grasp an object with the palmar side of the hand and not with the back of the hand. Previous research has focused independently on the impacts of each on exogenous visuospatial attention (Lloyd et al., 2010; Reed et al., 2010) yet it is important to establish their combined impact because such differences in intrinsic representation co-occur. That is, intrinsic representation either the dominant and non-dominant hand is concurrently impacted by handedness and grasping affordances.

The second study was designed to investigate systematically, how exogenous visuospatial attention is directed relative to the functional properties of the hands. That is, to compare the speed of reflexive attention shifts to objects near the hands, relative to the handedness of the participant, and whether the objects are presented to the grasping or non-grasping surface of the hand. The second study focussed specifically on how these factors shape the distribution and shifts of attention in near-hand space using a covert cueing paradigm (Posner & Cohen, 1984). To this end, study two also evaluated whether such intrinsic factors influenced response profiles. In particular, whether the manual response measure employed by many studies of near hand attention, is itself impacted by intrinsic representation of the hand. This is based on preliminary evidence for stimulus-response compatibility effects associated with the dominant hand of both left and right handers (Rubichi & Nicoletti, 2006). That is, individuals are faster to make responses to objects aligned with their dominant hand (e.g. right handers are faster to respond to right aligned targets with their right hand and the reverse for left handers).
Abstract

We examined how factors related to the internal representation of the hands (handedness and grasping affordances) influence the distribution of visuospatial attention near the body. Left and right handed participants completed a covert visual cueing task. In Experiment 1, participants discriminated target shapes, responding with either their dominant or non-dominant hand. In Experiment 2, the non-responding hand was positioned below one of two target placeholders, aligned with the shoulder. In Experiment 3 the near-monitor hand was positioned under the placeholder in the opposite region of hemispace, crossed over the body midline. For Experiments 2 & 3, in blocked trials the palmar and back-of-hand surfaces were directed towards the target placeholder such that targets appeared towards either the graspable or non-graspable space of the hand respectively. In Experiment 2, both left and right handers displayed larger accuracy cueing effects for targets near versus distant from the graspable space of the right hand. Right handers also displayed larger response time cueing effects for objects near the graspable versus non-graspable region of their dominant hand but not for their non-dominant hands. These effects were not evident for left-handers. In Experiment 3, for right handers, accuracy biases for near hand targets were still evident when the hand was crossed over the body midline, and reflected hand proximity but not functional orientation biases. These findings suggest that biased visuospatial attention enhances object identity discrimination near hands and that these effects are particularly enhanced for right-handers.
A substantial body of research has shown changes to the distribution of visuospatial attention towards objects when they are near hands. Specifically, the location of our hands, their posture and individual differences such as handedness all have demonstrable impacts on how visual attention is distributed to objects near the body (Abrams & Weidler, 2014; Abrams, et al., 2008; Adam, et al., 2012; Davoli, et al., 2010; Festman, Adam, Pratt & Fisher, 2013; Lloyd, et al., 2010; Reed, et al., 2010; Reed, et al., 2006). In addition, how we plan to use our hands to act upon objects in our environment (action goals), also impact near-body visual processing (Rizzolatti, et al., 1981; Tipper, et al., 1998). Typically, the measurement of near-hand attention confounds the goal of the action with the proximity of the hand. For example, experiments often have one hand adjacent to the display with the distant hand responding to the target (Festman et al., 2013; Lloyd, et al., 2010; Reed, et al., 2010; Reed, et al., 2006) or, alternatively, both hands adjacent to the display responding to targets (Abrams, et al., 2008; Adam et al., 2012; Davoli, et al., 2010).

By contrast, studies with non-manual response measures (i.e. saccade / foot-pedal) disambiguate the action goal from manual responses, but still do not assess directly the impact of the action goal on the effects found. As a result, it is difficult to disambiguate which elements of the action system contribute near-hand visuospatial attention in each case. The aim of the present research was to systematically investigate how the relationship between the goal of the action and two internal states of the action system: handedness and graspability influence the distribution of attention to objects near the body.

Handedness provides an index of the internal representation of our primary effectors, the hands. It plays an important role in determining how we use our hands to interact with objects in our environment. Right-handers as a group tend to be strongly right lateralised and use their right hand for most unimanual tasks whereas left-handers are heterogeneous in their degree of laterality overall and may use either hand depending on circumstance (Buckingham, Main, & Carey, 2011; Gardner & Potts, 2010; Gentilucci, Daprati, & Gangitano, 1998b). Importantly, left and right-handers differ in the neural representation of their dominant and non-dominant hands. The degree of dominance is a reflection of this representation (Amunts, et al., 1996; Volkmann, et al., 1998). Imaging studies have shown that the volume of motor cortex dedicated to the dominant hand is directly correlated with degree of handedness. In vivo recordings have shown that there is also greater synaptic connectivity in regions of motor cortex that represent the dominant hand compared with those that represent the non-dominant hand (Amunts, et al., 1996; Volkmann, et al., 1998). Thus, handedness provides a behavioural indicator of structural
and functional variations in the brain that manifest in differences in a variety of other cognitive domains and it is for these reasons that left handers are often excluded from cognitive research (Amunts, et al., 1996; Geschwind, 1984; Sörös, et al., 1999).

Importantly, evidence suggests that the relationship between handedness and experience is bidirectional. The frequency or familiarity we have with using a given hand modulates the perceptual processing of near body stimuli. For example, handedness influence which hand we use to complete an action (Aboitiz, Scheibel, Fisher, & Zaidel, 1992; Corballis, 1980; Geschwind, 1984). When we use one hand more often than the other, as we do with our dominant hand, we reinforce its representation over the non-dominant hand (Amunts, et al., 1996; Volkmann, et al., 1998). Because left-handers tend to be less lateralisied than right-handers, sensorimotor representation of their dominant hand is not as substantial as in right-handers, but is also subject to changes relative to experience, such that if they use their non-dominant hand often, they strengthen its representation (Volkmann, et al., 1998).

There is recent evidence that handedness modulates basic elements of visual perception (Le Bigot & Grosjean, 2012; Rubichi & Nicoletti, 2006). Namely, target detection is more accurate for objects in proximity to the hands. In one study, left- and right-handed participants completed a non-speeded discrimination task (responding to the identity of a left, right or centrally aligned stimulus) while their dominant hand, non-dominant hand, both hands or no hand was adjacent to the monitor (Le Bigot and Grosjean, 2012). Compared with the no-hand condition, right handers displayed greater visual sensitivity for stimuli near their dominant hand but not their non-dominant hand. By comparison, left handers displayed similar sensitivity for their dominant and non-dominant hand rather than a mirror pattern of the right handed participants (Le Bigot & Grosjean, 2012).

Other intrinsic factors such as the functional properties of hands themselves (grasping capabilities) have also been shown to influence visuospatial attention (Abrams, et al., 2008; Creem-Regehr & Kunz, 2010; Holmes & Spence, 2004; Lloyd, et al., 2010; Reed, et al., 2006). For example, Abrams and colleagues (2008) found that when hands were held to either side of a display (and responses made using display mounted response buttons) both spatial and temporal shifts in visual attention slowed compared with when responses were made by the hands distant from the display, even when hands were obscured from view. Similarly, Lloyd, et al., (2010) used a covert exogenous cueing paradigm (Posner, 1980; see Figure 1) to investigate the influence of hand location on attention shifting. Right handed participants held either their dominant or non-dominant
hand beneath one of two target placeholders and responded via foot-pedal to target identity. The authors found a larger cueing effect (difference between valid and invalid RTs) for targets in the hand-adjacent versus hand-distant placeholder. When the participants’ hands were crossed over the body midline and adjacent to the opposite hemispace placeholder, there were attentional biases only for targets near the right (dominant) hand and not the left. Also using an exogenous cueing task, Reed and colleagues (2006) demonstrated visuospatial biases that were specific to hands and not just a result of an additive visual anchor provided by the hand. The participant’s own hand, a non-hand visual anchor or a fake hand were placed adjacent to one of two potential target locations whilst the task was performed. Targets that appeared in the hand-adjacent location were detected faster than those equidistant from fixation but distant from the hand irrespective of cue validity. Moreover, this bias was not present for the visual anchor which indicates it was specific to representation of the hand (Reed, et al., 2006).

Further evidence suggests that visuospatial attention is distributed near the body, relative to both the location and grasping affordances of hands. Specifically, visual objects are detected more rapidly when near the palmar ‘grasping’ surface of the hand compared with the back-of-hand (Chan, Peterson, Barense & Pratt, 2013; Reed, et al., 2010). To investigate this, Reed et al. (2010) had participants hold their hand with either their palm or back-of-hand directed towards one of two potential target locations in a visual cueing task. Irrespective of cueing, participants were faster to detect targets appearing to their palm compared with the back-of-hand. This suggests that visuospatial attention was engaged more rapidly to the palmar (versus back) surface of the hand, because targets appearing in that location are more actable, thus reflecting an affordance bias in attention distribution (Reed et al., 2010). More recent research provides additional evidence for changes in visual processing relative to the posture of hands. For example Thomas (2015) found that when hands were adjacent to a visual display, precision grip postures enhanced observer performance on a form detection task (spatial sensitivity) whereas power grasps postures enhanced motion detection (temporal sensitivity).

The above findings qualify the results of earlier studies because they suggest that the orientation of the hand in relation to the target has a differential effect on the allocation of attentional resources (Abrams, et al., 2008; Lloyd, et al., 2010). In the studies conducted by Reed, et al., (2006) and Abrams, et al., (2008) participants directed the palmar surface of their hand towards the screen for all conditions in which hands were held near the display. By comparison, Lloyd, et al., (2010) had participants direct the back-of-the hand towards the target location. Thus we do not have a clear understanding of which
attentional effects are attributable to mere hand proximity and which are related to the graspable properties of the objects. This is important because each has presented evidence that the location of the hand influences different mechanisms of visuospatial attention (engagement, shifting and spatial coding). For example, Abrams et al., (2008) showed that both spatial and temporal shifts in visual attention were slowed amongst visual objects near the hands. Reed et al., (2006; 2010) demonstrated faster engagement and Lloyd et al., (2010) found slower disengagement of attention for targets appearing near versus distant from the hand. Due to the different postures and response measures used in each, the functional orientation of the hand may contribute differently to each of these. It is also not possible to disambiguate whether the effects found by each reflect consistent visuospatial hand biases depending on task demands or the differential influence of the graspability of the targets. Moreover all of the described studies evaluated right-handed participants so it is unclear how intrinsic representation of the hands themselves may contribute to these effects.

This highlights another important consideration for paradigms which investigate hand proximity. All of the outlined intrinsic factors have been shown to influence the distribution of visuospatial attention in one manner or another. Yet in examining how attention contributes to near-body visual processing, we also need to take into account the response demands of the tasks used to evaluate these (e.g., to press a key in response to the onset of a target). Extrinsic factors such as the goal of the action (e.g., to depress a key following the appearance of a target or to discriminate the identity of an object) have also been shown determine how visual attention is distributed within near-body space. Neurophysiological and behavioural research has found that visual stimuli near the body are coded relative to action centred reference frames (Cosman & Vecera, 2010; Meegan & Tipper, 1998; Rizzolatti, et al., 1981; Tipper, et al., 1998; Tipper, Lortie, & Baylis, 1992). For example, Cosman and Vecera (2010) found that proximity of one or both hands to a visual object resulted observers more often identifying objects as foreground figures irrespective of the presence of contextual cues suggesting the object was concave (i.e. not in the foreground). These and similar findings suggest that rather than just being delineated by mere proximity to the body, visual objects are prioritised perceptually based on how we may use our hands to act on them or within the space that they are situated.

Neurons in ventral premotor cortex selectively activate to visual stimuli relative to their proximity to the hands. These neurons display maximal activation when stimuli are on or near the hands, or critically, when they move towards them (Rizzolatti, et al., 1981). In line with this, behavioural evidence has shown that action goals modulate attentional
selection. When the goal of an action is to reach from one point to another, visual inputs which fall within the zone between the start and goal location of the reach, are prioritised for attention (Baldauf, et al., 2006; Tipper, et al., 1998). The action itself defines the area of attentional prioritisation. For example, Tipper and colleagues (1998; 1998; 1992) found that response times (RTs) were slower when distractors were presented between the hand and target compared with visual objects that were near the body but not within the frame of the action (Meegan & Tipper, 1998; Tipper, et al., 1998; Tipper, et al., 1992).

The aforementioned research employed either the non-adjacent hand or both hands to respond to visual objects. Thus we cannot dissociate effects attributable to the manual action goal from those attributable to internal representation of the hand, because they share a bidirectional relationship. We can examine the spatial relationship between the action goal and the proximity of the hands to the target stimulus, and how that relationship modulates visuospatial attention is distributed near the body. In the present study we did so by systematically varying the relationship between the goal of the action and the proximity of the hand to examine the added contributions of handedness, hand posture and proximity. In Experiment 1 we examined how handedness influenced the distribution of visuospatial attention relative to the laterality of the response hand. Experiment 2 evaluated how the combination of hand proximity, posture and the laterality of the response hand influenced the distribution of visuospatial attention relative to handedness. Experiment 3 spatially dissociated the response hand from the hand adjacent to the monitor to evaluate whether lateralised biases remap with the location of the hand in the opposite region of hemispace.

**Experiment 1**

The aim of Experiment 1 was to provide a measure of baseline visuospatial biases relative to handedness. We examined how the relationship between the laterality of the response hand (left versus right) and handedness (left-handed versus right-handed) influenced the distribution of attention within a visual display, to ascertain whether any response-biases were present. Left and right-handed participants completed a Posner (1984) cueing task with predictable lateral cues responding to targets with either their dominant or non-dominant hand with both hands distant from the display. Because both hands were distant from the display, hand proximity and posture should not impact the pattern of results. Thus any resultant biases in visuospatial attention may be attributable to changes in visual attention based on handedness. We predicted that, irrespective of handedness, participants would display validity effects whereby responses would be faster
for validly versus invalidly cued targets as is the typical finding for this paradigm. If handedness influences the overall distribution of visuospatial attention, we would expect responses to be faster to targets when responding with their dominant versus non-dominant hand irrespective of cue validity (main effect of response hand). Alternatively, if handedness influences shifts in visuospatial attention, we would expect a greater cueing effect for targets aligned with the dominant hand, when participants responding with their dominant hand. Due to the greater degree of laterality exhibited by right handers it is also possible that right-handers would show more of an effect of response hand (dominant versus non-dominant) either via faster responses overall compared with left-handers when responding to targets with the dominant hand, or interacting with cueing to alter cueing costs.

Method

Subjects. Forty-two undergraduate students (25 females; 21 left-handed and 21 right-handed by self-report) from the University of Queensland (mean age 20.48 years) completed the experiment in return for course credit, all gave informed consent.

Stimuli and procedure. Stimuli were created in Microsoft PowerPoint and presented using E-Prime 2.0 at a 50-cm viewing distance on 32-cm × 48-cm LCD colour monitors (resolution of 1,680 × 1050 pixels). Two blue placeholder rectangles (7.44˚ × 5.73˚) with the far edge 24.27˚ from fixation were presented in the bottom corners or the monitor on a black background either side of a white fixation cross (0.5˚). A white peripheral cue box (6.87˚ × 5.15˚) appeared in one of the place holders. Targets were solid yellow shapes, either a triangle or circle (1.14˚) that appeared in centre of one of the placeholders, 20.96˚ from central fixation with spatial location (left or right) randomised across trials.

The fixation cross and placeholders appeared for 700 - 1000ms and remained on display when a 250ms duration cue appeared in either the left or the right placeholder. At cue offset, in replication of Lloyd et al., (2010) there was a 250ms stimulus onset asynchrony (SOA). The target (yellow circle or triangle) appeared in either the same location as the cue (valid cue) or the opposite location (invalid cue). Target location was invalidly cued on 30% of trials (Figure 1a) and validly cued on 70% of trials (Figure 1b). Participants were instructed to respond as quickly and accurately as possible to the target identity (circle or triangle; equally probable) by clicking either the left or right button on the computer mouse with their index / middle finger respectively, counterbalanced across participants.
Participants completed the task in a quiet, dimly lit room with their eyes approximately 50cms from the monitor. A subset of left and right handed participants were randomly assigned to complete the task with either their left hand (11 left handed participants; 10 right-handed participants) or right hand (10 left handed participants; 11 right-handed participants) resting on the table, 40cms from the centre of the monitor. The hand not engaged in completing the task was rested in the participants lap. Of the right handed participants; five responded to triangles with their index finger and circles with their middle finger and six with the reverse. Of the left handed participants; five responded to triangles with their index finger and circles with their middle finger and six completed the task with the reverse arrangement.

Results and Discussion

Anticipatory RTs < 150ms (0.29%) and non-stimulus driven RTs > 1000ms, (1.29%) were also excluded (see Table 1 for summary of mean RTs and accuracy for each level of each condition).

RT analysis. A mixed repeated measures ANOVA was conducted with the within subjects factor target location (left target; right target) and the between subjects factors of handedness (left handed; right handed) and response hand (left; right). Cueing effect, computed as the invalid RTs – valid RTs, was the dependant variable. The only significant finding was a main effect of target location $F(1,38) = 10.28, p = .003$, $\eta^2_p = .21$. There was a greater cueing effect for left versus right sided targets, irrespective of handedness and response hand. No interactions reached statistical significance.
Table 1. Mean RTs (in ms), with standard errors (in parentheses), percentages of accuracy, for left and right handed participants, separated by response hand (left, right), target location (hand distant, hand adjacent), and cue validity (valid, invalid).

<table>
<thead>
<tr>
<th>Handedness</th>
<th>Response hand</th>
<th>Target location</th>
<th>Cue validity</th>
<th>Cueing effect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>RT</td>
<td>Valid</td>
<td>Invalid</td>
</tr>
<tr>
<td>Left</td>
<td>Left</td>
<td>554.16(28)</td>
<td>.97</td>
<td>.92</td>
</tr>
<tr>
<td></td>
<td>Right</td>
<td>549.48(27)</td>
<td>.95</td>
<td>.96</td>
</tr>
<tr>
<td>Right</td>
<td>Left</td>
<td>567.08(31)</td>
<td>.95</td>
<td>.91</td>
</tr>
<tr>
<td></td>
<td>Right</td>
<td>566.33(33)</td>
<td>.97</td>
<td>.98</td>
</tr>
<tr>
<td>Right</td>
<td>Left</td>
<td>551.36(30)</td>
<td>.97</td>
<td>.96</td>
</tr>
<tr>
<td></td>
<td>Right</td>
<td>572.49(28)</td>
<td>.97</td>
<td>.94</td>
</tr>
<tr>
<td>Right</td>
<td>Left</td>
<td>571.58(30)</td>
<td>.95</td>
<td>.90</td>
</tr>
<tr>
<td></td>
<td>Right</td>
<td>576.95(31)</td>
<td>.96</td>
<td>.93</td>
</tr>
</tbody>
</table>

Error analysis. We conducted a mixed repeated measures ANOVA with the same factors as the RT analysis. Accuracy cueing effect served as the dependant variable. This was computed as the mean accuracy for validly cued targets minus the mean accuracy invalidly cued targets. The analysis revealed a main effect of target location $F(1,38) = 7.79, p = .008, \eta^2_p = .17$. There was a larger cueing cost for left versus right targets, consistent with the changes in RT. We interpret these results as a reflection of stimulus-response compatibility effects related to the use of the computer mouse for which the more frequent usage is a left click (Peters & Ivanoff, 1999; Tucker & Ellis, 1998b). Importantly, the above findings suggest that there was no demonstrable impact of handedness, or the laterality of the response-hand on covert exogenous attention. Thus, intrinsic differences in body representation related to handedness and hand laterality did not likely influence how attention was distributed/shifted when performing a distal task.

Experiment 2

Experiment 1 rules out any effect of handedness on the distribution of visuospatial attention in a covert orienting paradigm. Following from this, the aim of the second
experiment was to systematically examine the combined influence of handedness, hand proximity and functional orientation of the hand (i.e. whether the palm or back-of-hand was oriented towards the display) on the distribution of visuospatial attention. We adopted posture elements from the methodologies of Lloyd et al., (2010) and Reed et al., (2006), presenting the palmar (grasping) and back-of-hand (non-grasping) surfaces towards one of two target placeholders (in blocked trials) whilst keeping the hand location constant across postures. The participant’s hand was positioned below the monitor directly under one of the two target placeholders with either the palmar or back-of-hand surface oriented upwards (towards the target placeholder). Thus when targets appeared in the hand-adjacent location they were either in graspable or non-graspable space of the hand.

Participants held either their dominant or non-dominant hand directly under the placeholder that corresponded with the hand side (e.g., right hand place under the right placeholder) and we compared performance between left and right-handed participants.

In this experiment, we aimed to establish which is perceptually important as a cue for attention: the relationship between the hand near the display and the target, or the relationship between response hand and the target or any combination of these. We predicted that the proximal hand would be weighted as the stronger cue for visuospatial attention. If this is the case there should be evidence of attentional prioritisation (faster RTs and improved accuracy) for targets near versus distant from the hand, more so when the grasping versus non-grasping region of the hand is oriented towards the display, as a reflection of attentional prioritisation relative to grasping affordances. Moreover, these effects should be more pronounced (in the form of greater cueing effects) when the proximal hand is dominant compared with non-dominant, as a result of greater structural and functional representation (Amunts, et al., 1996). Alternatively, if the goal of the action is the primary driver for visual attention, changes to visuospatial attention should be evident when the dominant hand is responding.

Method

Subjects. Forty-six undergraduate students (35 females; 21 left-handed and 24 right-handed by self-report) from the University of Queensland (mean age 19.79 years) completed the experiment in return for course credit, all gave informed consent.

Stimuli and procedure. These were identical to those of Experiment 1 with the exception of the following. Of the right handed participants, 10 responded to triangles with their index finger and circles with their middle finger and 11 with the reverse. Of the left handed participants; 11 responded to triangles with their index finger and circles with their
middle finger and 11 completed the task with the reverse arrangement. Participants completed two blocks of 128 trials (256 total) one with the hand grasable (Figure 1a) and one with the hand non-graspable (Figure 1b) with block order counterbalanced across participants.

Half of the participants positioned their left hand under the left bottom corner of the screen and responded to targets with their right hand (left hand proximal) and the other half positioned their right hand under the right bottom corner of the screen and responded to targets with their left hand (right hand proximal). Postures and time-courses are shown in Figure 1. In the grasping condition, the hand was positioned directly under one of the target placeholders with the palm oriented towards the placeholder (Figure 1a). In the non-grasping condition, the hand was positioned directly under one of the target placeholders with the palm oriented towards the placeholder (Figure 1b).

**Figure 1.** Hand postures and trial progression for Experiment 2. Figure 1A) represents the graspable posture, figure 1B) represents the non-graspable posture.

**Results and Discussion**

Participants with overall accuracy < 70% (2 participants, both right-handed) were excluded from further analyses. This resulted in 11 left-handed and 11 right handed participants completing the task with their left hand adjacent to the display and 11 left-handed and 10 right-handed participants completing the task with their right hand adjacent to the display. Anticipatory RTs < 150ms (0.13%) and non-stimulus driven RTs > 1000ms,
(5.98%) were also excluded (see Table 2 for summary of mean RTs and accuracy for each level of each condition).

**RT analysis.** A mixed repeated-measures ANOVA was conducted on the mean RTs the within subjects factors of target location (hand adjacent; hand distant), hand posture (non-graspable; graspable) and the between subjects factor of handedness (left handed; right handed) and proximal hand laterality (left; right). As computed in Experiment 1, RT cueing effect was the dependant variable.
Table 2. Mean RTs (in ms), with standard errors (in parentheses), percentages of accuracy, for left and right handed participants, separated by hand side (left, right), target location (hand distant, hand adjacent), hand posture (non-graspable, graspable), cue validity (valid, invalid) and mean cuing effect.

<table>
<thead>
<tr>
<th>Handedness</th>
<th>Hand side</th>
<th>Hand posture</th>
<th>Target location</th>
<th>Cue validity</th>
<th>Cueing effect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Invalid</td>
<td>Valid</td>
</tr>
<tr>
<td>Experiment 2</td>
<td>Left</td>
<td>Left</td>
<td>Non-graspable</td>
<td>Distant</td>
<td>615.38(23)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>%</td>
<td>.90</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Adjacent</td>
<td>639.41(36)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>%</td>
<td>.91</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Graspable</td>
<td>Distant</td>
<td>638.99(28)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>%</td>
<td>.91</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Adjacent</td>
<td>625.43(27)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>%</td>
<td>.93</td>
</tr>
<tr>
<td>Right</td>
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| Right | Non-graspable | Distant | RT  | 735.31(47) | 620.04(32) | 97.51(26) |
|       |   | % | .94 | .98 | .03 |
| Adjacent | RT  | 703.88(38) | 628.57(33) | 116.40(35) |
|       | % | .96 | .97 | .01 |

| Right | Non-graspable | Distant | RT  | 693.83(38) | 596.32(28) | 115.28(29) |
|       |   | % | .96 | .95 | -.01 |
| Adjacent | RT  | 714.05(43) | 597.66(30) | 75.31(25) |
|       | % | .98 | .95 | -.02 |

| Right | Non-graspable | Distant | RT  | 684.20(58) | 591.81(45) | 38.81(26) |
|       |   | % | .88 | .92 | .04 |
| Adjacent | RT  | 671.33(47) | 589.54(43) | 92.38(30) |
|       | % | .96 | .94 | -.01 |

| Right | Non-graspable | Distant | RT  | 688.52(45) | 625.39(42) | 81.79(31) |
|       |   | % | .88 | .93 | .05 |
| Adjacent | RT  | 654.29(45) | 615.49(40) | 63.12(30) |
|       | % | .96 | .96 | -.00 |

<p>| Right | Left   | Non-graspable | Distant | RT  | 610.92(44) | 553.27(30) | 95.26(24) |</p>
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There was an interaction between hand posture, target location, and proximal hand laterality $F(1,42) = 5.81, p = .020, \eta_p^2 = .12$. We compared between proximal hand laterality groups for each level of hand posture and target location and found larger cueing effects for the non-graspable hand distant condition for the right proximal hand laterality versus left proximal hand laterality $t(44) = 2.85, p = .007, d = .39$.

To examine handedness effects directly, we conducted separate ANOVAs for each handedness group with the factors, hand posture, target location and proximal hand laterality. We found no significant differences for left handers. For right handers, there was a trending interaction between hand posture, target location and proximal hand laterality $F(1,42) = 4.06, p = .057, \eta_p^2 = .17$. Follow-up planned comparisons were conducted comparing the graspable and non-graspable postures for each target location (two comparisons per handedness group). For right handed participants with the right proximal hand laterality, there was a larger cueing cost when targets appeared near versus distant from the hand when the hand was in the graspable posture $t(20) = 2.53, p = .032, d = .49$. No other effects reached significance.

**Error analysis.** Mean error was evaluated by comparing cueing effects (valid-invalid accuracy) in a mixed ANOVA with the within subjects factors of target location (hand adjacent; hand distant) and hand posture (non-graspable; graspable) and the between subjects factor of handedness (left handed; right handed) and proximal hand laterality (left; right). There was a main effect of target location $F(1,42) = 8.52, p = .006, \eta_p^2 = .17$. Cueing effects were larger for hand adjacent versus hand distant targets. There was also a main effect of hand posture $F(1,42) = 4.91, p = .032, \eta_p^2 = .11$, with larger cueing effects for the graspable versus non-graspable posture, consistent with a visuospatial bias relative to grasping affordances.

An interaction between target location and hand posture clarified the above main effects $F(1,42) = 8.00, p = .007, \eta_p^2 = .16$. Follow-up t-tests compared target locations between hand postures. These revealed larger cueing effects for objects distant from versus adjacent to the grasping region of the hand $t(42) = 2.66, p = .001, d = .38$. In addition, there was also an interaction between hand posture and proximal hand laterality $F(1,42) = 5.37, p = .025, \eta_p^2 = .11$. We followed this up by comparing between proximal hand laterality groups (left; right) for each hand posture. There was a greater cueing cost for the graspable posture when the right versus left hand was proximal $t(25) = 2.49, p = .042$. 

There was also a three-way interaction between hand posture, target location and hand under the monitor $F(1,42) = 5.93, p = .019, \eta_p^2 = .12$. To follow this up, we compared proximal hand laterality groups for each level of hand posture and target location (4 comparisons). Cueing effects were larger for targets distant from the graspable region of the hand when the right versus left hand was proximal $t(23) = 2.49, p = .020, d = .46$ (see Figure 3 for graphical representation). Taken together, these findings suggest that there was enhanced ability to discriminate target identity, when targets onset near the graspable region of the right hand, compared with both the non-graspable region. Moreover, they indicate that there was impairment of processing for targets which onset distant from this region.

To examine effects related to handedness, we conducted separate ANOVAs with the within-subjects factors hand posture, target location and proximal hand laterality for each handedness group. As with the RT findings, we found no significant differences for left handers. For right handers there was a main effect of target location $F(1,20) = 6.25, p = .021, \eta_p^2 = .24$, cueing effects were larger for hand adjacent versus hand distant targets. We also found an interaction between hand posture and target location $F(1,20) = 4.79, p = .041, \eta_p^2 = .19$, however no follow-up pairwise comparisons reached statistical significance. There was an interaction between hand posture and hand-under the monitor group $F(1,20) = 5.96, p = .025, \eta_p^2 = .23$. This was followed up by comparing between proximal hand laterality groups for each hand posture. There was a greater cueing cost for the non-graspable posture when the left versus right hand was under the monitor $t(20) = 2.39, p = .026, d = .47$. 
Figure 2. Accuracy cueing cost by target location, hand posture and handedness. Graphs (A) and (C) display mean cueing cost (with standard error bars) for left handers with their (A) left hand near and (C) right hand near. Graphs (B) and (D) display mean cueing cost (with standard error bars) for the right handers with their (B) left hand near and (d) right hand near the display.

The findings of Experiment 2 indicate that there are biases in near-hand attention relative to the grasping affordances of the hand which influence the observer’s object identification accuracy. When considered in combination with the RT results, these findings suggest that visuospatial attention is biased to the grasping space of the right hand. As a result there are enhancements in identifying objects in this location and associated impairments in identifying targets in opposite the site of biased attention. For right handers specifically, the results also suggest that there is speeded engagement and delayed disengagement of attention to the graspable region of the dominant hand. In line with this, the results provide further evidence that left-handers do no display mirror attention biases for their dominant hand than do right handers. Instead the current findings
suggest that left-handers also have greater accuracy in detecting objects near the graspable space of the right hand. This may reflect use-specific changes in representation, as left handers must often employ their non-dominant hand to complete tasks, due to the fact that many every-day objects (e.g., door handles) afford action from the right hand. However, it is important to note that when broken down by handedness group, these effects dissipate which suggests that strong dominant hand grasping-space biases in right-handers may drive this attentional bias.

**Experiment 3**

In Experiment 2, we found that the functional representation of the right hand, when proximal to the display, influenced the distribution of visuospatial attention. The results showed that accuracy of object identification was enhanced near the palm of the right hand and right handers also displayed faster engagement and delayed disengagements of attention to the grasping space of the dominant hand. The aim of Experiment 3 was to examine whether such visuospatial biases remain when the hand is crossed over the body midline, and thus are specific to functional representation of the limb.

In many instances in everyday life, we use our hands in an ipsilateral location or towards the body midline. Yet we are also capable of using hands to complete actions in the opposite region of visual hemispace; crossed over the body midline (Schieber & Santello, 2004). Hand-specific visuospatial biases have been interpreted by earlier research to be a reflection of the response properties of bimodal neurons (Cosman & Vecera, 2010; Reed, et al., 2004; Reed, et al., 2010; Reed, et al., 2006; Rizzolatti, et al., 1981). Attentional biases result from the overlapping visual and tactile representation of the space near the hand. If it is the case then the biases found in Experiment 2 should occur irrespective of the hands location in visual space. Moreover, it is important to establish whether the laterality of targets (relative to the hand) and observer handedness impact attentional distribution in space.

We used a similar methodology to Experiment 2 but the dominant or non-dominant hand under the contralateral rather than ipsilateral target placeholder. We predicted that if the visuospatial and response biases found in the second experiment were due specifically to internal representation of the right hand and not to an overall lateralisation bias, we would expect that the findings to will be replicated when the hands cross over the body midline. That is, we should find the same cueing effects for targets appearing near the right hand now in the contralateral region of visual space.
Method

Subjects. Thirty-five undergraduates (21 females; 19 right-handed; 16 left-handed by self-report) from the University of Queensland (mean age 22.14 years) participated in return for course credit or for AUD10 paid remuneration, all gave informed consent.

Stimuli and procedure. Stimuli and procedure were identical to Experiment 2 with the following exceptions. Participants crossed either their right or left hand (randomised between participants) over the midline and held it under the opposite corner of the monitor (see Figure 3 for diagrammatic representation). Of the right handed participants; five responded to triangles with their index finger and circles with their middle finger and four with the reverse. Of the left handed participants, four responded to triangles with their index finger and circles with their middle finger and four completed the task with the reverse arrangement.

Results and Discussion

Participants with overall accuracy < 70% (3 participants; all right-handed) were removed from further analyses. Anticipatory (< 150ms, < .001%) and non-stimulus driven (> 1000ms, 0.05%) RT trials were excluded from latency and accuracy analyses. Ten right handed and 9 left handed participants completed the task with the left hand adjacent to the monitor and 8 right handed and 8 left handed participants completing the task with their right hand adjacent to the monitor (see Table 2 for summary of mean RT and accuracy for each level of each factor).

RT analysis. We conducted a mixed ANOVA with the same factors as the RT analysis for Experiment 2. There were no significant findings. To examine how handedness influenced the distribution of attention we conducted separate ANOVAs by
handedness group (left; right) using cueing cost as the variable of interest. No main effects or comparisons reached statistical significance.

**Error analysis.** We conducted a mixed ANOVA with the same factors as the error analysis for Experiment 2. These revealed an interaction between target location and handedness $F(1,31) = 4.79, p = .036$, $\eta^2_p = .13$. Follow up t-tests compared mean accuracy for each target location between handedness groups. Consistent with the results of Experiment 2, this revealed that right handers had a greater cueing cost for targets appearing on the hand side, compared with those appearing opposite the hand $t(33) = 2.50, p = .017$, $d = .39$. To examine how handedness influenced accuracy we conducted separate ANOVAs by handedness group (left; right) using accuracy cueing cost as the dependant variable. For left handers there was a main effect of target location $F(1,15) = 4.81, p = .045$, $\eta^2_p = .24$, such that there was a larger cueing effect for targets distant from versus adjacent to the hand (see Figure 4). No other effects reached significance. For right-handers there were no significant differences.
Figure 4. Accuracy cueing cost by target location, hand posture and handedness. Graphs (a) and (c) display mean cueing cost (with standard error bars) for left handers with their (a) left hand near and (c) right hand near. Graphs (b) and (d) display mean cueing cost (with standard error bars) for the right handers with their (b) left hand near and (d) right hand near the display.

The above findings suggest that hand-centred bias in accuracy remained when hands were crossed over the body midline. This was such that object discrimination was more accurate for objects which onset near the right hand compared with those distant from it, irrespective of handedness. However, there was no longer any evidence for graspable biases for the right hand. This may be due to the reduction in the actionable value of the hand when crossed over the body midline, or to the increased difficulty of completing the task with the hand in a crossed posture. That is, the posture undertaken with the hand crossed over the body midline and the grasping side of the hand (palm) was oriented towards the display, reduces the capability for grasping. The crossed position makes grasping awkward and therefore may reduce the relevance of the hand orientation.
as a cue for visuospatial attention. While it is still possible to grasp an object in this posture, it is a less posturally comfortable action than the uncrossed position. Thus the affordances typically conveyed to the object near the hand by the orientation of the palm may be reduced. In turn, this may mitigate the significance of the palm orientation as a cue for attention. In addition, the results of Experiment 3 suggest that left handers no longer exhibit grasping biases for the right hand or generalised biases in the accuracy of object discrimination relative to the proximity of either the dominant or non-dominant hand, when hands are crossed over the body midline.

General Discussion

The aim of the present research was to investigate how grasping affordances and handedness work in combination with action goals to influence the distribution of visuospatial attention near hands. Experiment 1 found that when completing a distal task, exogenous cues modulated attention. Handedness or the laterality of the response hand, conversely, do not influence attention systematically. Experiment 2 found that the grasping affordances of the right hand, when proximal to a visual display, biased shifts in visuospatial attention. Both left and right handers displayed greater accuracy costs when detecting objects near versus distant from the palm of the right hand. Importantly, there were handedness differences such that right handers also displayed more rapid engagement slower disengagement of visuospatial attention to hand-adjacent targets near the graspable region of their dominant hand. Experiment 3 found that when hands were crossed over the body midline, only right-handers retained dominant hand biases in the accuracy of target identification, and grasping space biases were no longer apparent. Taken together, these findings provide evidence that visuospatial attention is distributed to objects near the hands, relative to grasping affordances and the strength of the underlying representation.

The current research presents a number of novel findings relating to the distribution of visuospatial attention near the body. Foremost, we extended upon the findings of Reed and colleagues (2010) by showing that when the task requires a higher-order aspect of visual processing (shape discrimination versus onset detection), hand location and posture modulated shifts of attention. Importantly we also illustrated that such attentional biases enhanced object identification at the site of the attention shift, and impaired object identification in the unattended zone. The aforementioned changes in visuospatial attention run somewhat counter to the overall biases in the distribution of visuospatial attention found by Reed and colleagues (2010).
Those authors found that observers were faster to detect objects near the palm of their hands, irrespective of cue validity and hand laterality (Reed et al., 2010). We propose that this is likely the result of the discrimination (as opposed to detection) task employed in the present research. With regards to task demands, the difference between target detection and discrimination is that the latter requires focal attention whereas the former does not (Sagi & Julesz, 1985). Specifically, object shape discrimination requires a higher order judgement of object properties than detection does, and as a result great attentional resources to discern target identity. Thus, the present findings likely reflect that internal representation of hands relative to handedness and grasping capability enhances focal attention which in turn facilitates object processing. This is a critical finding because it speaks to the level of attentional processing that is affected by the functional properties of the hands. When considered in combination with the findings of Reed et al., (2010), it appears that visual objects may be detected more rapidly when adjacent to the hands, but there are additive attentional benefits to processing object properties when they are graspable.

Our results support the proposal by Lloyd and colleagues (2010) that right-lateralised biases in attention shifting evident in their research, were most likely the result of hand dominance in their sample. We extended on these by investigating a left-handed sample and found that left handers do not display the mirror attentional biases for their dominant hand that right-handers do. Instead we showed that left-handers also display biases in visuospatial attention relative to the location and functional orientation of the right hand. Also, we found that visuospatial biases for right-handed subjects are restricted to the dominant (right) and did not affect performance when the non-dominant hand was proximal to the display. The present findings further clarify those of Lloyd and colleagues (2010) because they show that shifts of attention to the dominant hand occur relative to the grasping affordances of the right hand, when ipsilaterally versus contralaterally aligned.

The functional account of near-body attention posits that the allocation of additional attentional resources near the hands serves to enhance the cognitive processing of action-relevant stimulus properties (Abrams & Weidler, 2014; Reed, et al., 2010; Reed, et al., 2006). These in turn are thought to guide sensorimotor transformations required to act on hand-adjacent objects (Goodale, 1990; Goodale & Milner, 1992). We extended upon this to show that biases in near-hand attention were associated with enhancements in object identification, to the detriment of locations distant from the hand which supports the improved perception for action hypothesis. Thus, the current findings provide a more specialised picture of the visuospatial attention biases by illustrating that they are not only
relative to handedness but also to grasping affordances. These results further suggest that visuospatial biases are likely the result of expertise dependant changes to visual perception rather than solely a reflection of strengthened right hand representation in right-dominant people. When considered in combination, the findings of Experiment 2 and 3 suggests that graspable biases in visuospatial attention do not occur in contexts where the orientation of the hand in relation to the stimulus makes grasping awkward.

Following from the above, we have shown that the underlying strength of limb representation is not the sole factor driving near-hand attention. The majority of near-hand attention research has focused primarily on right handers. The current findings contribute to understanding of body representation by demonstrating that mirrored biases are not displayed by left handers. Instead we found evidence for right-hand grasping space biases and no evidence for dominant hand associated biases in visuospatial attention for left handers. One possible explanation for these effects is that left handers are more heterogeneous in terms of the degree of hand laterality compared with right handers (Amunts, et al., 1996; Geschwind, 1984; Oldfield, 1971). Thus it may be the case that the lack of significant differences found in the present study between the two groups is a reflection of this heterogeneity. Moreover, the current findings, particularly with regards to Experiment 2, may reflect use-specific changes in visuospatial attention. Because left handers exist in a world designed to afford actions for the right hand, this may as a result have enhanced the underlying representation of right-grasping affordances, as was evident in the present study.

Moreover, it is also likely that left handers exhibit changes to visuospatial attention based on the functional properties and proximity of their hands but that these do not impact the mechanisms of attention probed in the present task paradigm. Earlier evidence provides support for lower level perceptual differences in the representation of the dominant and non-dominant hand between left and right handers. For example, Le Bigot and Grosjean (2012) demonstrated that left handers display greater visual sensitivity (d’) for objects near both their dominant and non-dominant hand. When considered in combination with the present findings, this indicates that differences in visuospatial attention may stem or be contributed to underlying changes in visual sensitivity. Thus it is important for future research to establish which mechanisms of visual perception and visuospatial attention are impacted by left-hand dominance, because they appear to be less lateralised than those evident for right handers.

To sum, the current study has shown that intrinsic representation of hands, both with regards to the strength of underlying representation and actable properties, modifies
the distribution of visuospatial attention near the body. Our results suggest that there are biases in visuospatial attention relative to the grasping properties of hands which serve to enhance the identification of objects in this space. We have also shown that this occurs to the detriment of perceptual processing of objects which appear near to the body, but distant from the hand. These findings extend current understanding of near body attention because they demonstrate that both proximity and functional orientation of the hands play critical roles in directing visuospatial attention. Thus future research regarding near-hand attention and perception must account for the impact of both on effects of interest.
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CHAPTER 4: GRASPING REMAPS THE DISTRIBUTION OF VISUOSPATIAL ATTENTION AND ENHANCES COMPETING ACTION ACTIVATION
In the previous two studies I have examined how the relative location of the hands impacts the distribution of visuospatial attention within peripersonal space. Study 1 focused specifically on how hands proximity impacted endogenous attention. Study 2 extended on this to examine how underlying representation of the hands impacts earlier reflexive shifts in attention. The pattern of results reported provides additional support for the account of near-hand visual processing whereby attention is distributed to objects near the body based on their ‘actability’. That is, relative to the underlying representation of the limb, and the actable properties of objects near the body such as their size and dimensions. These findings also indicate that subsequent higher-order attention biases directly facilitate the processing of action relevant stimulus properties.

Together, these findings paint a picture that the functional properties of hands, bias shifts in visuospatial attention and that subsequent attentional engagement enhances perception for action. These effects are consistent with the embodied theory of cognition as they show that representation of the body shapes processing of the visual environment, even when one is not actively using the limb in question to act on the objects being observed (Bridgeman & Tseng, 2011; Reed, et al., 2004; Rizzolatti, et al., 1981). The aim of the third study in the thesis was to extend on this by investigating how specific action goals contribute to the perceptual processing of objects and specifically our ability to suppress the processing of irrelevant stimuli near the body. In particular, to extend on the evidence from studies of static hands and examine how the body in action influences the top-down attention set. On the other side of this, the study also aimed to investigate how such top-down attention set impacts the execution of goal directed actions.

A critical consideration for investigations of near-hand visual processing, is that visual environments are not only processed when hands are static. Manual action necessitates the movement of the limbs through space and importantly must account for changes in the visual environment. The findings of Study 2 suggest that when static there are exogenous biases in visuospatial attention which aid in the attentional capture of objects that may be graspable. Behavioural research by others has also shown that the trajectories of goal directed reaches actions can update relative to changing actions goals or changes in the visual environment during execution of planned actions, to avoid potential objects (Grafton et al., 1996). Taken together, these findings suggest that exogenous attention capture by objects near the hands may have a discernible impact on how actions are subsequently executed. Moreover, this suggests that in addition to demonstrable bottom-up modulations of visuospatial attention found for objects which
onset near static hands, there are additional top-down changes in the distribution of visuospatial attention, relative to manual action goals.

Earlier research provides evidence of attentional demarcation of visual space relative to the location of planned reaches. This takes the form of greater attention capture and competing action activation for non-target objects which onset within the frame of action compared with those which onset equidistant from the body but not within the frame of action (Baldauf, et al., 2006; Meegan & Tipper, 1998; Tipper, Howard, & Jackson, 1997; Welsh, Elliott, & Weeks, 1999). Importantly, this indicates that there are top-down modulations of attention which serve to prioritise visual inputs relevant to subsequent reach trajectories. In study three, I aimed to extend upon these by evaluating not just how the location of the reach itself impacts the distribution of attention, but how the goal of the reach end point (to point to versus to grasp an object) influences the attentional priority placed on objects within the frame of action.

Another important consideration stemming from the dynamic nature of manual action is the there must be attentional prioritisation of new visual inputs which arise within the frame of action (between the start and end point of a planned reach) during action execution. This is because such objects may necessitate an updating of the reach trajectory if they represent obstacles to reaching the goal of the planned action. In line with this, study three also aimed to examine the direct relationship between top-down modulations of attention capture relative to action goals and subsequent sensorimotor transformations. In this way, the third study was designed to examine the other side of the relationship between perception and action proposed by the integrative theory of attention; that in addition to action goals shaping near-body visual processing, subsequent processing of the visual environment would in turn shape sensorimotor output (Decety, Jeannerod, & Prablanc, 1989; Gibson, 1979). Here we evaluate firstly, whether action goals modify attention capture within the frame of action, and secondly whether subsequent reach profiles reflect this attentional prioritisation.
Abstract
We examined how action goals influence the distribution of visuospatial attention near the body (Experiment 1) and how the temporal relationship between the non-task relevant visual distractors and targets modifies shifts in visuospatial attention (Experiment 2). Targets were cylinders mounted with light emitting diodes (LEDs) in the left and right hemispace of a visual display. Following the illumination of either the left or right target LED, participants either reached to point-to or grasp the top of the target object in blocked trials. Coincident with onset of the target there was a distractor (smaller cylinder with mounted LED) in the same or opposite hemispace halfway between the initiation point and target, or no distractor appeared. In Experiment 1, during grasp reaches there was greater temporal distractor interference effects (slower reach initiation and greater overall trajectory deviations along the x-axis) compared with point reaches. In Experiment 2, distractor onset was either 200ms prior to (-200ms), coincident with (0ms) or 200ms following (+200ms) the target onset. For both point and grasp actions -200ms distractors were associated with greater interference effects compared with 0ms and +200ms. For grasp reaches +200ms distractors were also associated with larger temporal interference effects compared with 0ms. -200ms distractors were associated with reach trajectories that were more deviated compared with coincident and +200ms for pointing actions. For grasping actions they resulted in greater trajectory deviation - 200ms distractors compared with coincident conditions. These findings suggest that grasping actions remap the distribution of visuospatial attention to prioritise objects in the frame of action compared with pointing reaches. Moreover perceptual uncertainty regarding the layout of actable space influences grasping reach trajectories to a greater degree compared with pointing reaches.
To reach out and grasp an object near our body requires perceptual processing of both the object that we plan to grasp, and our environment (Milner & Goodale, 2006). For example, when you grab your favourite mug from the cupboard, you need to take into account how you plan to pick up the mug (i.e., by the handle or the body – the action goal) as well as the proximity and size of the surrounding mugs and where the mug is situated in the cupboard (the action space) to be able to successfully pick it up without it slipping out of your hand or knocking over the other mugs in the process. Both the action goal and the action space influence the path that the reach will take to the mug (trajectory) and the scaling of your digits. As this example illustrates, how we plan to act upon an object, determines what visual information in the environment is relevant to guiding manual action at any given time (Baldauf, Wolf, & Deubel, 2006; Beckering & Neggers, 2002; Brozzoli, Cardinali, Pavani, & Farnè, 2010; Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009).

Neurophysiological and behavioural research has shown that there is selective processing of visual information relevant to action execution, based on the goal of the action. Yet, human actions are dynamic (Goodale, 1990; Goodale, Milner, Jakobson, & Carey, 1991). We are capable of changing action-goals part way through execution (e.g., deciding to grasp two mugs rather than one) or maintaining an action goal in the face of a changing environment (e.g., altering the path of the reach to grab our favourite mug whilst avoiding the arm of another person reaching for a mug in the same cupboard) (Castiello, 1996; D’Ausilio, Brunetti, Delogu, Santonico, & Belardinelli, 2010; Humphreys et al., 2010). As a result of this flexibility, the processes which underlie action must be capable of updating with changing action goals and circumstances. In the present series of experiments we investigated how the goal of the actor, the immediate environment, and their interaction affects the execution of manual actions. In particular, we examined how visual attention is distributed to the space near the body relative to action goals and, critically, how such distribution updates to incorporate new visual information.

In the brain, specialised multisensory neurons, primarily in premotor cortex, subserve the representation of the ‘actable’ space near the body (peripersonal space). Such neurons are characterised by overlapping visual and tactile receptive fields which update during movement to represent the space that surrounds a specific body part, such as the hand (Calvert, 2001; Duhamel, Colby, & Goldberg, 1998; Fogassi et al., 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, et al., 1981). Generally, the peripersonal zone encompasses the space within thirty centimetres of a given body part (Rizzolatti, et al., 1981). Neurophysiological and behavioural evidence indicates that the functional purpose of representing this near-body zone in premotor cortex is to map the
sensorimotor information required for the execution of object-based actions (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Duhamel, et al., 1998; Farnè & Làdavas, 2000; Godschalk, et al., 1985). Accordingly, response profiles of bimodal neurons are tuned to body proximity such that firing increases in magnitude as visual inputs move towards the body, and decreases as they move away (di Pellegrino, Ladavas, & Farne, 1997; Fogassi, et al., 1992; Graziano & Gross, 1994; Graziano & Gross, 1998; Rizzolatti, et al., 1981). This provides evidence that peripersonal neurons process sensory inputs from body-part-centred frames of reference.

Sub-populations of peripersonal neurons also encode the type of action that an organism plans to execute (Gallese, et al., 1996; Gardner et al., 2007; Godschalk, et al., 1985; Roy, Paulignan, Farnè, Jouffrais, & Boussaoud, 2000). For example, firing patterns in single-cell recordings in macaque monkeys are consistent with a subset of action-relevant bimodal neurons. These sub-populations only fired on presentation of a food item when the macaque reached to retrieve it and not when the food item was presented in the same location and subsequently provided to the macaque by the experimenter (Godschalk et al., 1985). Critically, the same populations showed further modulations in their activation profiles relative to the reach-type required to retrieve the food item, either a full-hand grasp or fine-tuned pincer grip which suggests that visual objects are encoded relative to their actable properties (Godschalk, et al., 1985). These findings are consistent with visual objects in peripersonal space being represented in premotor cortex relative to the sensorimotor requirements of actions. That is, objects are processed relative to their proximity and the manner in which they will be acted upon so that visual inputs related to the size and position of the object inform the generation of the goal directed action.

The above results indicate that within premotor cortex there is overlapping representation of both the space near the body, and the goal of the actor. This has implications for attention because visual attention is captured by multisensory stimuli in peripersonal space, more so than in extrapersonal space. In turn, the top-down deployment of attention to a particular target can facilitate multisensory integration (see Talsma, et al., 2010 for review). This provides a picture of a bidirectional relationship between perception and attention to facilitate action (Gondan, Blurton, Hughes, & Greenlee, 2011). In line with this, convergent behavioural findings have demonstrated that the goals of manual actions (for example reaching to grasp versus merely point-to an object) modulates when in the process of action planning, co-occurring multisensory inputs are integrated. That is, the goal of an action defines whether inputs from different sensory modalities are represented as part of peripersonal space, and perceived as related to a
single event or object (Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008; Gondan, et al., 2011).

Brozzoli et al., (2010) investigated this using a tactile-discrimination task with targets presented on either the forefinger or thumb (which represented an upper and lower location respectively) whilst an observer reached to point to or grasp an object mounted with visual distractors. Distractors were either congruent (same location up or down) or incongruent (opposite location up or down) with the tactile target location. The target - distractor pairing was presented either before (static condition), at the initiation of (initiation) or during (execution) a reach to point-to or grasp an object. For both pointing and grasping reaches, participants displayed greater visuotactile integration (larger differences between congruent and incongruent response times) compared with the static condition. Critically, visuotactile integration occurred to a greater extent for grasping versus pointing reaches when the distractor appeared during the execution phase of the action. These findings suggest that making goal-directed reaches perceptually updates the relationship between visual and tactile inputs before the hand touched the object such that peripersonal space extends to include the target object, based on the goal of the action. Importantly, grasp facilitates visuotactile integration more than pointing during action execution, indicating online remapping of peripersonal space to accommodate not just the location being reached to but also the sensorimotor requirements of the action. This is particularly important for grasping context because the actable properties include the dimensions of the target object itself.

Action goals modulate both how visual attention is distributed to non-target objects near the body as well as how subsequent actions are executed. In the context of manual actions, the relationship between the hand and the target object defines the frame of action (Colby, 1998; Meegan & Tipper, 1998). Behavioural research has shown that non-target ‘distractor’ objects between the initiation and end-point of a reach are prioritised in attention over those still near to the body but outside of the frame of action. (Baldauf, et al., 2006; Tipper, et al., 1998; Tipper, et al., 1997; Tipper, Lortie, & Baylis, 1992). For example, studies of reach kinematics have found that when we reach into crowded visual environments, we process the visual properties of objects within the frame of action to a greater extent compared to those outside of it (Beldauf & Deubel, 2006). The distribution of visuospatial attention within the frame of action is crucial because it facilitates further cognitive processing of objects that are being acted on and those that are relevant to action. In a series of seminal studies, Tipper and colleagues (1992; 1998; 1997) demonstrated that the distribution of visuospatial attention in action space was defined by
the location of reach and that visual objects between the start and end point of the reach capture attention more so than those outside of the action frame. In one study, observers reached to depress buttons that corresponded in location with the onset of a target light emitting diode (LED) (Tipper, et al., 1992). Distractor LEDs were illuminated either between the start point of the reach and the target (within the frame of action) or distant from both (i.e., outside of the frame of action). The authors found that onset of a distractor LED between the hand and the target resulted in slower response times compared with distractors outside of the frame of action (Tipper, et al., 1992).

In a similar study, investigating the influence of non-target distractors on reach kinematics, observers reached to grasp a physical object placed in one of two potential target locations in the presence of distractors (LEDs) which illuminated within or outside of the frame of action (Tipper, et al., 1997). For distractors within action-space, reaches were initiated slower and their trajectory deviated away from the distractor location. Importantly, when participants were made aware in advance of the target location, they displayed interference effects only for distractors directly between the start and end point of the reach. These findings indicate that there is attentional and sensorimotor prioritisation of non-target stimuli when they are within the frame of action (between the start and end point of a reach) even when such distractor objects do not represent direct obstacles to the action (Meegan & Tipper, 1998; Tipper, et al., 1998; Tipper, et al., 1997; Tipper, et al., 1992). Critically, they also suggest that such attentional and kinematic biases are driven, in part, by perceptual uncertainty. More time is taken to plan the reach, and greater deviation is seen in the reach trajectory when we are uncertain of the layout within which we are acting.

The primary perceptual explanation for changes to reach trajectories and reach onset under conditions where non-obstacles appear within the frame of action, is that non-target objects activate competing responses (Tipper, et al., 1998; Tipper, et al., 1997; Welsh & Elliot, 2004). That is, based on their proximity to the body and their presence within the frame of action, distractors activate competing action plans that must be inhibited prior to the onset of the reach. This perceptual explanation ties in with research on object action affordances which have consistently demonstrated that the structural morphology of an object and proximity to the body, activates specific motor actions. Tucker and Ellis (1998) illustrated this using a stimulus-response compatibility task in which the participant responded by key press to images of objects that were action congruent (e.g. saucepan handle oriented towards) or action incongruent (e.g. handle oriented away) relative to the response hand. Responses were faster to action congruent than action
incongruent objects (Tucker & Ellis, 1998b). Critically, electrophysiological evidence has found that such motor preparation occurs as early as 400ms prior to action execution which indicates that bindings of vision and action occurs early in the sensory pathways (Goslin, et al., 2012). For example, recordings from event related potentials (ERPs) during completion of a stimulus-response compatibility tasks results in greater lateralised rapid motor preparation (as evidenced by early readiness potentials, 100-200ms after stimulus presentation) for the hand afforded by the object orientation.

Similar affordance effects, in the form of competing response activation, have also been demonstrated for goal directed reaches (Welsh & Elliott, 2004; Welsh, et al., 1999). In one study by Welsh and Elliott (1999) participants reached to depress keys that corresponded with a target LED, when distractor LEDs were presented between the start and end point of the reach, or beyond the frame of the reach. However, contrary to the findings of Tipper and colleagues, (1992; 1998) reach trajectories deviated towards rather than away from the distractor location when distractors were presented temporally close to the target (within 250ms) (Welsh & Elliott, 2004). Yet when distractors were temporally displaced from target for long enough for participants to inhibit a competing response (presented either 750ms prior to or following the target) reach trajectories did not deviate towards the target location (Welsh & Elliott, 2004). Based on these findings Welsh and Elliot (2004) proposed a complimentary theory for action activation in the frame of action. Specifically, they proposed that if responses are inhibited prior to movement execution, the subsequent reach trajectory will deviate away from the competing distractor. By comparison, if distractor inhibition is not complete prior to the competing response reaching the threshold of activation, the subsequent reach trajectory will deviate towards the distractor before correcting to reach to the target.

Recent behavioural evidence confirms that greater visuospatial attention within the frame of action, enhances perceptual processing of objects therein and critically, accounts for multiple objects (Bekkering & Neggers, 2002; Beldauf & Deubel 2006). Visuospatial attention is biased towards multiple target locations during the preparation and execution of goal-directed reaches such that it facilitates accurate visual discrimination of objects within the frame of action. In one experiment participants reached to two or three pre-cued visual targets arranged in a clock-face around the reach start point (Beldauf & Deubel 2006). Concurrently they completed a two alternative forced-choice (2AFC) number/ letter discrimination task with the 2AFC target presented at either at the location of one of the reach-targets, between the reach targets (within the frame of action), or a different location on the clock-face (i.e., not within the frame of action). The accuracy of 2AFC discrimination
was higher for stimuli presented on and between the reach locations compared with those outside of the action frame. This indicates that visual attention was distributed to all target locations during action preparation (prior to action execution) in parallel rather than serially. That is, attention was distributed to multiple goal locations prior to the execution of the first action rather than shifting during action execution to each goal in turn. Importantly, targets which appeared between the multiple reach locations (within the frame of action) were attentionally prioritised as well. This suggests that pre-established action goals modified how visual attention was distributed during action execution, similar to the effects found by investigations of peripersonal space and action (Brozzoli, et al., 2010; Fischer, Prinz, & Lotz, 2008; Moskowitz, 2002).

Further evidence suggests that the goal of actions impact which elements of visual distractors are perceptually prioritised (Bekkering & Neggers, 2002). Bekkering and Neggers (2002) found that when participants had to either point to or grasp target objects in a visual search display they made fewer saccades to objects which had a different orientation to the target when grasping versus pointing. This indicates that there is overt attentional prioritisation of action-relevant features for visual distractors. Similarly, work by Welsh and Pratt (2008) has also shown that the properties of visual objects that capture attention are modulated by the type of response the observer must make (e.g. respond with a keypress versus a goal directed reach). The authors found that offset distractors caused temporal interference to keypress responses for onset targets, but not goal directed reaching responses in the same condition. These findings suggest that response expectations influence top-down attentional set, and thus the observer’s ability to suppress irrelevant distractors. Further, they indicate that goal directed reaching enhances such suppression more so than making keypress responses.

These and similar findings suggest there is contingent capture for near body objects (Folk, Remington & Johnston, 1992). That is, the goal of an action defines an action-specific frame of reference which includes the target object and any other objects between the initiation and end point of the reach. Thus, objects which appear within this space capture attention because they are within the frame of action. Moreover, objects that are either being acted upon or which may influence the execution of a planned action are prioritised and have resulting impacts on the trajectories of reaches within this zone.

Beyond this, evidence from peripersonal space research suggests that multisensory near-body representation updates relative to action goals as well as during action execution to incorporate new sensory information (Brozzoli, et al., 2010; Godschalk, et al., 1985). This has implications for the distribution of visuospatial attention because it
suggests that there are online perceptual processes which update the representation of near body space relative to the changing visual environment. Current evidence suggests that the directionality of this relationship is such that the goal of the action defines top-down attentional set. The goal of the action defines action space, and visuospatial attention is distributed to this space to enhance processing of action relevant inputs whether they be related to the target itself, potential obstacles or non-obstacles that are present in the frame of action. As a result, non-target objects within this space capture attention more than those outside of it, and they modify the trajectory of reaches accordingly.

Yet a number of factors relating to the relationship between the distribution of visuospatial attention and the resulting motor output remain unclear. These include the goal of the action itself influences the attentional priority given to distractors within the frame of action (as evidenced by the time taken to plan the reach and the extent of competing action activation) and how action goals influence competing activation. The present study had two overarching aims. The first was to establish whether action goals influence sensorimotor interference from distractor objects within the frame of action. Specifically, whether reaches which require grip scaling influence the observer's ability to suppress non-obstacle distractors compared with non-grasping reaches. The second was to evaluate whether the attentional mechanisms involved in distributing attention in the action space are dissociable from those responsible for updating the action plan once an action is already underway. That is, how the distribution of visuospatial attention (relative to the action goal) contributes to the extent of competing action activation expressed in the reach.

To examine the first aim we utilised reach-to-point and reach-to-grasp as our two action goals. While both actions follow similar reach paths at the outset there are also concrete biomechanical and kinematic differences in action execution, as well as different implications for the objects being reached towards such that the location of the target is relevant to both, but object dimensions are relevant only to grasp (Carnahan, Goodale, & Marteniuk, 1993; Castiello, 2005; Grafton, Fagg, Woods, & Arbib, 1996). From a biomechanical perspective, the only component of a pointing reach is the transport movement of the arm and subsequent hand movements, such as extending a digit, which occurs as an extension of the arm movement. By comparison, grasping reaches consist of transport and grasp components (Jeannerod, 1984) and require fine-tuned movement of the distal grasp effectors (grip-scaling) in combination with the transport component (Jeannerod, 1984; Nordin & Frankel, 2001). Thus, the properties of the object such as size
and dimensions are relevant to the planning stage of grasp but not point reaches (Borchers & Himmelbach, 2012; Brozzoli, et al., 2010; Brozzoli, et al., 2009; Gallese, et al., 1996; Grafton, et al., 1996; Haffenden & Goodale, 2000; Hesse, de Grave, Franz, Brenner, & Smeets, 2007; Jakobson & Goodale, 1991; Roy, et al., 2000).

In relation to the above factors, we investigated how the added relevance of the object-based visual inputs changed the way that non-target objects were processed. To address the second aim, we examined how attention was distributed to distractors within actable space when they onset before, coincident with or following the presentation of the target, but within temporal proximity to the target so to enable examination of competing action activation.

We evaluated two elements related to the 'goal' aspect of goal-directed reaches. The first was how the actor plans to interact with the target: to point or grasp (hereafter referred to as the action-goal). The second was the location of the end-point of the reach, i.e., where the target was situated on the display in relation to the distractors. This was operationalised in the current study as either in the left or right region of the display board (hereafter referred to as the action-target). The evidence outlined above suggests that action-targets and non-target distractors influence perceptual processing during reach planning by biasing shifts of attention (Baldauf, et al., 2006; Bekkering & Neggers, 2002; Brozzoli, et al., 2009; Tipper, et al., 1992). Thus, by investigating action-targets we can draw inferences about the how visuospatial attention is shifted to the objects in the display. By comparison, investigating action-goals allows us to infer how the actor’s intentions modulate the representation of peripersonal space during action execution (Brozzoli, et al., 2009).

Experiment 1

The aim of the first experiment was to examine how action goals influence the distribution of visuospatial attention in action space. To measure the impact of action goals we examined distractor interference effects reflected in reach initiation times and deviations in reach trajectories. With regards to these measures, Tipper and colleagues (1992) found that actions comparable to reach-to-point actions (reaching to depress a key) were slower to execute when visual distractors were presented within the frame of action compared with those outside of the frame of action. In their later study evaluating reach to grasp, they found that for grasping actions, reach trajectories deviated away from the same distractors (those within the frame of action) compared with when distractors were presented outside of the frame of action or when there were no distractors (Tipper et al.,
Yet subsequent research by Welsh and Elliot (2004) indicates that the trajectory of reaches (either movement towards or away from the distractor location) are specific to competing action activation when distractors are presented in close temporal proximity to the target. Thus, in the first experiment we aimed to elicit competing action activations and examine whether the goal of the action, to point to or grasp an object modulates the actors ability to suppress competing actions. In blocked trials, participants reached to point-to or grasp the top of one of two visual targets (LEDs) in the presence or absence a visual distractor (another LED). In randomised trials within each block, visual distractors appeared on either the same side (same-side) or opposite side (opposite-side) from the target object or remained off (no-distractor). Importantly, both distractors were located half-way between the initiation point of the reach and the target, so were within the frame of action but outside of the direct reach trajectory to the target and thus were not obstacles.

To examine visuospatial attention we assessed two elements of goal-directed reaches. The first was whether the action goal modulated how attention was shifted to distractors within the frame of action. Time to initiation (from the onset of the target) was the temporal measure of distractor interference because it allowed us to infer two indices. First, time to initiation is a proxy for stimulus processing and action planning time, allowing comparisons between costs in attention shifting brought on by the non-obstacle distractors in the different locations. Accordingly, initiation time indicates how different target-distractor pairings (action targets) and the goals of action modify attention distribution. For example, if reach initiation times are delayed in some versus other conditions, we can infer that the distractors have either captured attention prior to its shift to the target location which in turn has delayed or impacted the planning and execution of the reach. This is in line with earlier research which has shown that attention is distributed to the action-relevant stimuli in the display prior to the development of the action plan, to facilitate visuomotor transformations (Colby, 1998; Corbetta & Shulman, 2002; di Pellegrino, et al., 1992). Second, by comparing distractor interference effects between point and grasp reaches, we can make inferences about how action goals modulate the distribution of attention within the frame of action, prior to the onset of the action. Tipper and colleagues (1992; 1998) proposed that distractor interference reflects action specific prioritisation. Under this explanation we predicted that same side distractors would elicit larger distractor interference effects than opposite side distractors. Moreover, we predicted an interaction such that this difference would be more pronounced for grasp versus point reaches. This is in line with the reasoning that grasp reaches require grip scaling thus distractors should be prioritised more so than for point reaches.
We also examined whether the goal of the action modulates the extent of action affordances (and in turn competing response activation) elicited by the appearance of the distractors. In line with Tipper et al. (1998) and Welsh and Elliot (2004) we investigated deviations along the X-axis from the theoretical straight line between the initiation point and target. This allowed us to evaluate how pointing versus grasping influence competing response activation for the different target-distractor configurations, through analysis of direct motor output. Grasp reaches are more complex than simple pointing reaches because they, require the programming and execution of the parameters of the grasp component (separating then closing together of the thumb and fingers; Jeannerod 1984). Given this added biomechanical and kinematic complexity, we propose that distractor interference effects will be larger for these compared with pointing reaches. This is because non-target objects between the initiation and end point of a grasping reach may interfere with grip scaling, whereas for pointing actions this will not be the case. Accordingly, we predicted that irrespective of distractor location, reach deviations would be greater for point versus grasp reaches. With regards to competing response activation, we predicted in line with the findings of Welsh and Elliot (2004) that because targets and distractors were presented in temporal synchrony, competing action activation would result in reach deviations towards the distractors. Moreover, we predicted that this effect would be more pronounced for grasp versus point reaches.

**Method**

**Participants.** Twenty-one undergraduate students from the University of Queensland (mean age = 20.43; 16 females) completed the experiment in return for course credit. All were right handed as indicated by the Edinburgh Handedness Inventory and were naive to the aims of the experiment.

**Apparatus and Stimuli.** Two Dell PC computers were used to run the experiment. Stimuli presentation and motion capture recording were controlled using MATLAB software and Cogent toolbox. Two 10cm long, 5mm wide pieces of black wooden dowel provided target objects. These were mounted into a black display board and a single 5v red diffuse LED (with a luminance of 41cd/m²) was mounted to the top of each and provided the visual target stimuli (see figure 1). An initiation point was marked on the board and target objects were mounted 20cms in front and 10cms to the right and left of the initiation point at a visual angle of 28º (see Figure 1 for diagrammatic representation). The two distractor objects were two single 5v diffuse LED (with a luminance of 41cd/m²) presented atop 2.5cm long pieces of wooden dowel. Distractors were located halfway between the
initiation point and the target, (10cms in front and 10cms to the right and left of the initiation point) at a visual angle of 53º. LED illumination was controlled via a custom driver (JK Kinetics, USA).

Reach kinematics were recorded via a ProReflex (Qualisys) motion capture system, which comprised of three infrared cameras mounted to the front and sides of the display. Reflective markers were mounted to the fingernails of the thumb and forefinger, as well as to the radius and ulna of the participants’ right hand. Motion capture cameras recorded X, Y and Z coordinates of the markers, sampling at 100 frames per second, with accuracy at < 0.3mm.

**Design and Procedure.** Participants were seated at the front of the display board (approximately 20cms from the initiation point). We did not restrict the head of participants, in line with previous research (Tipper, et al., 1992). There were three types of distractor trials: same-side, opposite-side and no distractor. For the same-side trials, the visual distractor on the same side of the display board as the target was illuminated concurrently with the target. For opposite-side trials, the visual distractor on the opposite side of the display board from the target became illuminated concurrently with the target. For no distractor trials, neither of the distractor objects became illuminated. In blocked trials, participants reached or pointed to the top of the target object (with their fingers in pincer grip posture – see Figure 1) or reached and grasped the top of the target object. The 108 trials were divided into six blocks each of 18 trials, three blocks of grasping, and three of pointing, with block order counterbalanced between participants. Distractor-type was randomised within each block.
Figure 1. Diagrammatic representation of the display set-up A) illustrates the display layout and participant posture at the beginning of each trial. Figure B) illustrates a reach-to-point and C) a reach-to-grasp.

In reach-to-point trials, participants began each trial with their index and thumb of their right hand resting on the initiation point in gentle opposition (see Figure 1) and following a random pre-trial period of 1600-2000ms, the target was illuminated and the participant reached to either point to or grasp the target object (see Figure 1b and 1c). Participants were instructed to reach as soon as they saw that the LED mounted to the top had become illuminated and were instructed to ignore the visual distractors. They reached directly to the target object and held their point/grasp at the target location for a self-timed two-second interval before returning to the initiation point. Both the target and distractor remained illuminated until the end of the trial (3000ms following target onset). In reach-to-grasp trials, the procedure was identical except participants reached to grip the top of the target object with their thumb and index in a pincer grip posture.

Results and Discussion

Kinematic and timing parameters were calculated and compiled using MATLAB software. Time to initiation was calculated as time (in milliseconds) to movement onset.
from the illumination of the target. X-max deviations were calculated by plotting a hypothetical straight line from the start point of the radius to the radius’s location at the endpoint of the movement (the target location) and calculating the maximum deviation (in millimetres) of the radius towards the right (following a natural trajectory for right-hand reaches) from that straight line.

**Timing Parameters.** For time to initiation, we analysed distractor interference by computing a reach initiation cost. This was done by subtracting the mean response time for the no-distractor condition from the mean response time of the same-side and opposite-side distractor conditions for each level of reach type and target location. Time to initiation was analysed using a two block type (point, grasp) by two target location (left, right) by two distractor type (same-side, opposite-side) repeated measures within subjects analysis of variance (ANOVA).

**Table 1.** Reach initiation time costs by reach type, target location and distractor type.

<table>
<thead>
<tr>
<th>Reach type</th>
<th>Target location</th>
<th>Distractor type</th>
<th>Mean RT (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Point</td>
<td>Left</td>
<td>Same-side</td>
<td>8.86 (66)</td>
</tr>
<tr>
<td></td>
<td>Opposite</td>
<td>Same-side</td>
<td>.08 (36)</td>
</tr>
<tr>
<td>Right</td>
<td>Same-side</td>
<td>18.67 (126)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Opposite</td>
<td>-18.70 (93)</td>
<td></td>
</tr>
<tr>
<td>Grasp</td>
<td>Left</td>
<td>Same-side</td>
<td>-6.06 (34)</td>
</tr>
<tr>
<td></td>
<td>Opposite</td>
<td>24.18 (41)</td>
<td></td>
</tr>
<tr>
<td>Right</td>
<td>Same-side</td>
<td>-9.47 (43)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Opposite</td>
<td>.03 (47)</td>
<td></td>
</tr>
</tbody>
</table>

An interaction between reach type and distractor type $F(1, 19) = 8.38, p = .009, \eta^2_p = .31$ revealed that, contrary to prediction, for same-side distractors there was a smaller reach initiation cost for grasp ($M = -4.74, SE = 5.78$) versus point ($M = 16.34, SE = 6.06$) $t(19) = 3.23, p = .003, d = .59$. Overall there were also smaller grasp reach initiation costs for same-side ($M = -4.74, SE = 5.78$) versus opposite-side distractors ($M = 13.25, SE = 4.77$) $t(19) = 2.30, p = .033, d = .46$. For grasp reaches: when the distractor illuminated in the position nearest to the target, the time taken to plan and initiate the reach was significantly reduced compared to the pointing reaches. In addition, grasp reaches had significantly larger interference effects when an opposite-side distractor was illuminated compared with when a same-side distractor illuminated.

Initially, these findings appear contrary to the action frames of reference model proposed by Tipper et al., (1998). That model predicts that reach initiation would be more delayed for same versus opposite side distractors, because same side distractors are
more directly within the frame of the direct reach to the target. We believe, however, that the pattern obtained here can be taken as evidence that action goals shape the extent of attentional capture that distractors elicit when in the frame of action. Recall that Tipper et al., (1992) used pointing actions only, and that we are comparing pointing and grasping actions. We propose that distractors capture greater visuospatial attention in grasping compared with pointing. Thus, grasp reaches were initiated faster than point reaches when distractors were on the same side as the target. This is because, for same side distractors, whilst both target and distractor captured visuospatial attention, attention was distributed within the same region of hemispace. Visuospatial attention therefore was distributed over a smaller relative area for distractors which onset closer to the direct trajectory between the target and the initiation point compared with when they appeared in the opposite region of hemispace. This attentional capture was greater for grasp versus point reaches as reflected by faster reach initiation time. Consistent with this reasoning, we postulate that grasp reaches were delayed for opposite versus same-side distractors because attention was distributed to both the opposite-side distractor and target (over a larger region of visual space). This meant that attention must shift from the opposite side distractor to the relevant hemifield prior to reach execution, and because distractors captured greater attention for grasp reaches, this shifting cost was greater for grasp reaches.

The above findings are consistent with those of Tipper and colleagues (1992) in that they suggest that distractors within the frame of action activate competing action profiles which must be suppressed prior to action execution. Yet, for same-side distractors, these competing action profiles serve to enhance the profile (reduce deviations) of the reach towards the target, because they are congruent with the target reach action. We propose that grasping reaches, which are more complex than pointing reaches, result in greater perceptual priority being placed on non-target objects within the action space compared with pointing reaches.
Reach Trajectory Measures. For reach trajectory parameters we measured positive maximum x-deviation (how far the participant deviated in millimetres horizontally to the right of the direct path between the initiation point and target on the x-axis during the reach). We investigated this trajectory parameter as an indication of coding of movement direction - whether the participant was moving more to the left or right of the x-axis. On this measure, positive deviations reflect horizontal movement towards the right of the straight line between the initiation point and the target. Negative deviations reflect horizontal movements towards the left of the straight line between the initiation point and target. Importantly, x-positive deviation provides an indication of leftward deviation as well as rightward. X-positive deviations were computed by calculating the average deviation of the reach trajectory towards the right (during the course of the reach) from a hypothetical straight trajectory between the initiation point and target.

To investigate the influence of action goals on reach trajectories, we conducted a two block type (point; grasp) by two target location (left; right) by three distractor type (none; congruent; opposite-side) repeated measures within subjects ANOVA with maximum positive x-deviation in millimetres as the dependant variable (thus positive values represent rightward deviation, negative values represent leftward deviations). For this analysis, each distractor type was assessed (no distractor; same-side; opposite-side) rather than creating difference scores between the opposite-side and no-distractor trials so that we could evaluate whether reaches deviated towards or away from distractors.

Figure 2. Interaction between block type and distractor type for time to initiation with standard error bars ** $p < .001$. 
A main effect of reach type $F(1, 20) = 12.23 \ p = .002, \eta_p^2 = .38$ indicated that, consistent with prediction, overall maximum positive x-deviations were greater for grasping trials ($M = 26.35, \ SE = 1.23$) than pointing trials ($M = 22.12, \ SE = 1.40$). These findings are consistent with those of Tipper and colleagues (1997; 1992) and indicate that there is greater deviation (along a natural trajectory\(^1\)) for within action space distractors compared with no distractor. Moreover they extend on these findings by illustrating that grasp reaches, which require greater distal modulation such as grip-scaling, resulted in greater rightward deviations. A main effect of target location $F(1, 20) = 10.08 \ p = .005, \eta_p^2 = .34$, also revealed that there were greater deviations (i.e., movements towards the right) when reaching to right ($M = 27.52, \ SE = 1.10$) versus left sided targets ($M = 21.94, \ SE = 1.84$) similarly consistent with greater deviations along a natural trajectory for right-handed reaches.

An interaction between target side and distractor side $F(2, 40) = 11.91 \ p < .001, \eta_p^2 = .37$ revealed that for left-sided targets, there were greater rightward deviations for no distractors ($M = 25.00, \ SE = 1.46$) compared with same-side distractors ($M = 20.23, \ SE = 2.21$) and opposite-side distractors ($M = 20.60, \ SE = 2.17$; $t(20) = 3.37, \ p = .003, \ d = .60$ and $t(20) = 3.12, \ p = .005, \ d = .57$ respectively). This suggests that there was a more leftward (though still positive) trajectory for both distractor conditions compared with the no distractor condition. For right sided targets, there was greater rightward deviation for same-side distractor ($M = 29.30, \ SE = 1.15$) and opposite side distractor ($M = 27.77, \ SE = 1.28$) compared with no distractor ($M = 25.49, \ SE = 1.33$) trials $t(20) = 4.40, \ p < .001, \ d = .70$ and $t(20) = 2.67, \ p = .014, \ d = .51$ respectively. This interaction indicates that when distractors were present, participants consistently displayed greater deviation towards the target side compared with no distractors which replicates the trajectory changes found by Tipper and colleagues for within-action space distractors (1997).

However, this was further clarified by a three-way interaction between reach type, target location and distractor type ($F(2, 40) = 11.96 \ p < .001, \eta_p^2 = .37$). This revealed that for left targets with no distractor, the trajectory of the reach showed a greater rightward deviations for grasp trials ($M = 30.42, \ SE = 1.63$) compared with point trials ($M = 19.57, \ SE = 3.37$) $t(20) = 3.82, \ p = .001, \ d = .65$ (see Figure 3). This indicates that on the baseline no distractor condition, grasp reaches deviated more along a natural trajectory than point

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\(^1\) In the context of the current study a deviation along a natural trajectory refers to a deviation towards the right. This is because participants completed reaches with their right hands, which biomechanically deviate rightward during a straight reach (Fernandez & Bootsma, 2004; Nordin & Frankel, 2001).
reaches. For left sided targets with opposite-side distractors, there were greater rightward deviations for grasp ($M = 21.42, SE = 2.21$) compared with point trials ($M = 19.47, SE = 2.24$) $t(20) = 2.33, p = .030, d = .46$ which suggests, consistent with competing action activation, grasp reaches deviated more towards the distractor location (in the right hemispace) compared with pointing. However for right sided targets with opposite-side distractors, there were also more rightward deviations for grasp ($M = 30.09, SE = 1.50$) compared with point trials ($M = 25.44, SE = 1.40$) $t(20) = 3.33, p = .003, d = .59$. There are a number of possible explanations for this. First, reaches were deviating away from the distractor location (in the left hemispace which is contrary to what would be expected based on competing response activation (Welsh & Elliot, 2004). Second, it may be that as the actors were completing the task with the right arm, right sided stimuli produced stronger competing action activation. Activation of competing actions towards the distractor in the opposite region of hemispace may have been inhibited by the stronger affordances of the right sided targets. We propose this as the more likely explanation, given the greater rightward deviations found in the no distractor condition for grasp versus point reaches.

![Figure 3](https://example.com/f3.png)

**Figure 3.** Mean x-positive deviations in millimetres. Graph depicts the interaction between reach type, target location and distractor type with standard error bars **$p < .001$.**

Importantly, for same-side distractor trials there were no significant differences between pointing and grasping trajectories for either left or right targets. This indicates that
the greater rightward deviations for grasp reaches seen in the no-distractor condition are mitigated when targets and distractors onset within the same hemispace. This manifests in a relatively direct reach towards the target irrespective of action goal. That is, reaches were more leftward for left targets and more rightward for right targets when distractors and targets were in the same region of hemispace.

Taken together, Experiment 1 shows that both the target-distractor relationship and action goal influenced the distribution of visuospatial attention both in relation to initiation time and reach trajectory. Grasp reaches are initiated faster and display a more direct trajectory for same-side target and distractor pairings compared with point reaches. By contrast for opposite side distractors, reaches initiate later and, for left-sided targets, competing action activation is more apparent compared with point reaches.

**Experiment 2**

In the first experiment we found evidence that visual distractors within the frame of action are prioritised attentionally in grasping versus pointing. In addition, we found that competing action activation was enhanced for grasp versus point reaches. In Experiment 2, we evaluated how action goals modulate the actor’s ability to inhibit competing actions based on whether the distractor information onsets prior to the development of the action plan (before target location is known) versus when planning of the reach is already underway but the reach has not yet been executed (when target is known but the action space remains uncertain). A critical motivation for this was to establish when in the course of action planning and execution, distractors have maximum impact. In the first experiment, both the target and distractor were presented coincidentally. Thus the temporal relationship between the target and the distractor remained constant. At target/distractor onset participants were provided with information regarding the spatial relationship between the two, concurrently. Thus, attentional resources could be distributed to both in parallel prior to the development of the reach program (Baldauf et al., 2006).

Previous research has shown that visuospatial attention is distributed to objects near the body during action preparation in such a way as to prioritise those within the frame of action (Baldauf, et al., 2006; Tipper, et al., 1998). But many of the described tasks involved prior knowledge of the target locations or the coincident (or near coincident <100ms SOA) presentation of target and distractor prior to reach planning. Yet, evidence from Welsh et al., (1999; 2004) illustrates that when objects onset within a time period <500ms preceding or following the target, actors were unable to inhibit competing
responses and reach trajectories deviated towards non-target objects. Following from this, we aimed to assess how the goals of actions modulate the extent of competing action activation within the < 500ms time window. This is an important consideration because we often complete manual actions under dynamic situations and must adapt our action plan online to account for changes to the environment in which we are acting, or alternatively changes to the goal of the action.

Brozzoli et al., (2010) showed that the representation of near-body space updates online to facilitate the integration of related sensory inputs based on the sensorimotor requirements of action. They found that grasping results in remapping of peripersonal space more than pointing, to facilitate sensory integration of inputs relating to the object that will be grasped or interacted with (Brozzoli, et al., 2010). Importantly, this occurred when multisensory inputs appeared in close temporal proximity (<100ms SOA). One of the primary findings of this research was that visuotactile integration was greatest when concurrent inputs were presented during action execution, i.e., once the grasping reach had already been planned. This suggests that there is online monitoring of the visual environment during reach to grasp because the onset of a concurrent visual input is integrated with the tactile target on the hand. Moreover, the results indicate that the processing of near body stimuli is relative to the goal of an action at a given time. Changes to action goals are thought to drive these effects via top-down attentional modulation. In line with this, in Experiment 2 we aimed to examine directly how visuospatial attention contributes to this perceptual updating. We did this by comparing how the distribution of visuospatial attention updates/ changes relative the appearance of non-target objects which are temporally displaced (but within the <500ms action-inhibition time period) from the target but within the frame of action. Moreover we compared how visuospatial attention competing action activation for distractors in modulated each pointing and grasping reaches.

To investigate the above factors, we used three target-distractor stimulus onset asynchronies. In addition to the no-distractor and coincident distractor conditions used in the first experiment, distractors also appeared either 200ms prior to target onset (−200ms) or after target onset (+200ms) in line with evidence that visuomotor transformations and motor preparation for grasping occur between 100-150ms following stimulus (i.e. target) onset (di Pellegrino, et al., 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Rizzolatti, et al., 1981). Thus in the context of the distractor following conditions, the distractor onset occurred once the action plan had already been developed. In the context of the distractor preceding condition, the distractor was presented long enough prior to the target to benefit
from shifts in visuospatial attention (Posner & Cohen, 1984). The SOAs were randomised within trials of pointing and grasping to enable consideration of the role of action goals on visuospatial attention.

For the SOA manipulation, drawing upon the findings of Tipper and colleagues (1997) and Welsh and Elliot (2004), we predicted that there would be an increase in distractor interference for -200ms distractors compared with coincident with or +200ms distractors. This was based on the fact that awareness of the distractor location occurs prior to knowledge of the target location. Thus attention capture should be enhanced (relative to the 0ms and +200ms conditions) for both same-side and opposite side distractors because the target location may appear in either the right or left hemispace. Within this we also expected greater reach initiation costs for opposite-side distractors compared with same-side distractors (similar to the pattern found for coincident conditions) as a result of the need to shift attention from one hemispace to another before planning the reach following onset of the target.

With regards to reach trajectories, we predicted that -200ms distractors would elicit the largest competing response activations (as reflected by x-deviations) compared with 0ms and +200ms. In the +200ms condition, distractors onset once the reach plan had already been developed thus the appearance of the distractor prior to reach initiation (which typically occurs 400-700ms following target onset) will elicit competing motor preparation. Because the distractor appears within the inhibitory time frame established by Welsh and Elliot (2004) we expected this to result in greater competing action activation. This should result in reach initiation times which are comparable to the 0ms condition (and reduced compared with the preceding distractor condition) and reach trajectories that deviate more towards the distractor (compared with the 0ms condition) as a reflection of this poorer inhibition. In line with the findings of Experiment 1, we predicted that the described effects will be more exaggerated for grasp reaches, particularly in relation to reach trajectories for grasp versus point reaches, owing to the greater perceptual importance of objects within the action frame for the execution and digit scaling required in grasp reaches.

**Method**

**Participants.** Eighteen undergraduate students from the University of Queensland (mean age = 18.49; 11 females) completed the experiment in return for course credit. All were right handed as indicated by the Edinburgh Handedness Inventory and were naive to the aims of the experiment.
Apparatus and Stimuli. Apparatus and stimuli were identical to those in the first experiment. For each of the trials in which a distractor appeared (congruent and opposite-side) there were three stimulus onset asynchronies (SOA); distractor preceding target onset by 200ms (-200ms), distractor coincident with target (0ms) and distractor following target by 200ms (+200ms). We utilised the interval of 200ms to ensure that the distractor onset before action preparation for the target reach (-200ms) or directly after action preparation during the execution of the action (+200ms). For the 0ms trials, the distractor and target were presented for 3000ms, for the -200ms, the distractor was presented for 3200ms and the target for 3000ms, for the +200ms trials, the distractor was presented for 2800ms and the target for 3000ms.

Design and Procedure. These were identical to Experiment 1 with the exception of the following. The 252 trials in total were divided into six blocks each of 42 trials; three blocks of grasping and three of pointing with block order counterbalanced between participants. Distractor type (same-side opposite-side; no distractor) and SOA (-200ms, 0ms, +200ms) were randomised within block.

Results and Discussion

Timing parameters. Initiation times that were < 200ms (anticipatory < 1% of trials) and > 2000ms (not stimulus driven <3% of trials) were removed from the analysis. As with the first experiment, we computed the reach initiation cost by subtracting the no distractor initiation time from each of the distractor side (same side; opposite side) initiation time for each of the SOAs. Mean initiation time was assessed using a 2 Reach Type (Point, Grasp) by 3 SOA (0, +200, -200) by 2 Visual Distractor Side (same-side reach initiation cost, opposite-side reach initiation cost) repeated measures ANOVA.

There was a main effect of Distractor Side ($F(1, 17) = 5.99, p = .026, \eta_p^2 = .26$) such that participants had a smaller reach initiation cost for same-side ($M = 12.45, SD = 5.87$) versus opposite-side distractors ($M = 27.18, SD = 8.84$), consistent with the findings of Experiment 1. This provides further support for the proposition that visuospatial attention was captured by objects within the frame of action and thus there was a greater cost associated with shifting visuospatial attention from one hemifield to the other to attend to the target and plan subsequent actions.

There was a main effect of SOA ($F(2, 34) = 11.15, p < .001, \eta_p^2 = .40$) such that there were smaller reach initiation costs for 0ms SOAs ($M = -3.02, SD = 26.11$) compared with -200ms ($M = 51.89, SD = 64.09$) or +200ms distractors ($M = 10.57, SD = 20.89$; $t(17) = 3.60, p = .002, d = .66$ and $t(17) = 2.91, p = .010, d = .58$ respectively). Participants also
had smaller reach initiation costs for +200ms compared with -200ms \((t(17) = 3.02, p = .008, d = .59)\) target-distractor SOAs. This is consistent with the concept that distractor which onset after the target, appear after the action has already been planned, thus initiation times would be minimally affected by attention shifts to the distractor location. Also in line with our hypotheses, -200ms distractors resulted in delayed reach onset relative to both coincident and +200ms distractors.

**Table 2.** Reach initiation time costs by SOA, reach type, target location and distractor type.

<table>
<thead>
<tr>
<th>SOA</th>
<th>Reach type</th>
<th>Target location</th>
<th>Distractor type</th>
<th>Mean RT (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0ms</td>
<td>Point</td>
<td>Left</td>
<td>Same-side</td>
<td>-2.68 (39)</td>
</tr>
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<td></td>
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<td>Opposite-side</td>
<td>1.13 (51)</td>
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<td></td>
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<td>Right</td>
<td>Same-side</td>
<td>-8.52 (63)</td>
</tr>
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<td></td>
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<td>Opposite-side</td>
<td>-8.90 (60)</td>
</tr>
<tr>
<td></td>
<td>Grasp</td>
<td>Left</td>
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<td>37.80 (70)</td>
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<td></td>
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<td>Opposite-side</td>
<td>49.68 (98)</td>
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<td>68.24 (94)</td>
</tr>
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<td>+200</td>
<td>Point</td>
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<td>-3.59 (69)</td>
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<td></td>
<td></td>
<td>Opposite-side</td>
<td>55.96 (67)</td>
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</table>

The above findings imply first, that there is an overall temporal delay in shifting of visuospatial attention from the distractor to the target. Second they indicate that distractors within the frame of action captured attention more so when they appeared before the target compared with coincident with or following the target. This is consistent with both Tipper et al., (1992; 1997; 1998) and Welsh and Elliot (2004) and suggests that even
though distractors were non-predictive of target location, participants were unaware which target they were grasping towards, attention was still shifted towards the distractors in the display.

One surprising result was the smaller temporal cost associated with the coincident condition compared with the +200ms following condition indicating more delayed reaches when the distractor onset after the target. However, this finding was further clarified by interactions between SOA and Distractor Side \((F(2, 34) = 5.47, p = .009, \eta^2_p = .24)\). This revealed that for opposite-side distractors, participants had a smaller reach initiation cost when there was 0ms SOA \((M = -6.09, SD = 26.98)\) compared with -200ms \((M = 48.73, SD = 52.63; t(17) = 4.14, p < .001, d = .71)\). They also had a smaller reach initiation cost when same-side distractors illuminated +200ms \((M = -6.35, SD = 23.24)\) compared with -200ms \((M = 48.73, SD = 52.65; t(17) = 4.08, p = .001, d = .70)\). Similarly for same-side distractors, participants had a smaller reach initiation cost when there was no SOA \((M = -1.57, SD = 28.12)\) compared with -200ms \((M = 55.14, SD = 81.45; t(17) = 2.89, p = .011, d = .57)\) and compared with +200ms \((M = 27.86, SD = 35.12; t(17) = 3.48, p = .003, d = .64)\) but by contrast to opposite side distractors, there was no significant difference between the -200ms and +200ms condition. The described interactions contribute to the main effects by illustrating that there are greater costs associated with shifting attention to the target location when distractors are both temporally (onset prior to or following the target) and spatially displaced (appear in the opposite hemispace) from the target location.

**Figure 4.** Interaction between distractor onset at SOA with standard error bars. (**p < .005).
Reach trajectories. We investigated deviations along the x-axis by calculating the maximum horizontal positive deviation along the x-axis. Because we were interested in investigating how the timing of distractors influenced reach trajectories we compared SOAs (0ms, -200ms and +200ms) using a 2 reach type (point, grasp) by 2 distractor side (same-side, opposite-side)\(^2\) ANOVA.

A main effect of reach type \(F(1, 17) = 21.26\), \(p < .001\), \(\eta^2_p = .56\) revealed that, consistent with the findings of Experiment 1, participants deviated more rightward when grasping (\(M = 26.88\), \(SE = 1.33\)) versus pointing to the targets (\(M = 24.67\), \(SE = 1.79\)). In addition, a main effect of SOA \(F(1, 17) = 52.99\), \(p < .001\), \(\eta^2_p = 1.00\), found that participants made smaller overall rightward deviations for 0ms SOAs (\(M = 22.35\), \(SD = 6.21\)) compared with both +200ms (\(M = 28.91\), \(SD = 5.36\); \(t(17) = 7.83\), \(p < .001\), \(d = .88\)) and -200ms (\(M = 26.06\), \(SD = 5.79\); \(t(17) = 8.26\), \(p < .001\), \(d = .89\)). They also made smaller rightward deviations when distractors onset prior to the target (-200ms) compared with after the target (+200ms) \(t(17) = 5.04\), \(p < .001\), \(d = .77\). Trajectories deviated more when there was temporal asynchrony between the distractor and target compared with when both onset at the same time. Importantly, deviations were greatest when the distractor onset after the target. These findings are consistent with the model that distractors which onset after the target would activate greater competing responses compared with those proceeding or coincident with the target.

Importantly, action goals modulated competing action activation for the different target-distractor SOAs. An interaction between reach type and SOA \(F(1, 17) = 33.65\), \(p < .001\), \(\eta^2_p = .66\) revealed that for pointing reaches participants deviated more for +200ms (\(M = 29.21\), \(SD = 5.32\)) compared with 0ms (\(M = 21.89\), \(SD = 6.08\); \(t(17) = 8.04\), \(p < .001\), \(d = .89\)) or -200ms (\(M = 22.90\), \(SD = 6.62\); \(t(17) = 7.03\), \(p < .001\), \(d = .86\)). For grasping reaches, this pattern was slightly different: participants deviated more for -200ms (\(M = 29.21\), \(SD = 5.61\)) and +200ms (\(M = 28.62\), \(SD = 5.67\)) compared with 0ms (\(M = 22.82\), \(SD = 6.50\); \(t(17) = 8.16\), \(p < .001\), \(d = .89\) and \(t(17) = 6.41\), \(p < .001\), \(d = .84\) respectively.\(^3\)

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\(^2\) Because the no-distractor condition was the same for each of the SOAs, this was not included in the calculation of the omnibus ANOVA to enable comparisons of distractor effects between SOAs.

\(^3\) Analyses were conducted which included target location as a variable of interest, this same pattern of results was found for both left and right targets – see Appendix 1 for summary.
In relation to the SOA manipulation, in Experiment 2 we found that reaches deviated more when the distractor appeared after the target compared with before or coincident with it. When a visual object appeared within the frame of action subsequent to the reach planning, actors were unable to inhibit competing responses. When considered in combination with the findings regarding distractor interference, these results suggest there is an on-line correction of reach trajectories to compensate for the appearance of a distractor after the reach has been planned. However, because there was no interaction with distractor side, we cannot definitively state whether such deviations reflect a movement towards or away from the distractor location. Instead what the findings suggest is that when reaching to grasp, reaches deviate more along a natural trajectory both when distractors precede and follow the appearance of the target, yet for pointing reaches this is only the case when distractors precede the target.

**General Discussion**

In the present study we examined how visuospatial attention is distributed within near-body space relative to the goals of actions and the available visual inputs. To recap the primary findings: in Experiment 1, grasping reaches resulted in greater shifts of attention to distractors within the frame of action and greater competing action activation...
compared with point reaches. In Experiment 2, the temporal relationship between the
target and distractors modulated the impact of reach goals on selection of action-relevant
inputs. For pointing reaches, distractor interference effects were greatest when distractors
onset after the target compared with coincident and prior to the target. Reach trajectories
also reflected increased competing action activation for this condition. Grasping trials
displayed the same pattern of distractor interference as pointing trials, but reach
trajectories displayed greater distractor over-avoidance both when the distractor preceded
and followed the target relative to the coincident condition.

We present a number of novel findings, the most critical of which is that action goals
modify both the distribution of visuospatial attention within the frame of action, as well as
the extent that competing action activation influences subsequent reach trajectories. With
regards to visuospatial attention, the first major finding was that overall opposite-side
distractors delayed the onset of reaches more than same-side distractors. This was
particularly surprising given the current theoretical understanding of action frames of
reference, specifically that objects directly within the frame of action should elicit greater
distractor interference. The greater reach initiation costs for opposite versus same-side
distractors clarifies this because it demonstrates that objects within the frame of action are
subject to contingent capture (Folk, Remington, & Johnston, 1992). In the context of the
current study, targets and distractors were both luminance onsets. Thus in the case that
both onset at the same time (Experiment 1) both target and distractor must be attended
before one can be selected as target. Our findings are consistent with research on
attentional capture in three dimensional space which has illustrated that it is not possible to
set oneself for one depth plane (for example the target depth plane) and ignore another
(Finlayson, Remington, Retell, & Grove, 2013; Theeuwes, Atchley, & Kramer, 1998). The
current findings extend on this evidence by showing that reaching to grasp versus point to
an object, strengthens the contingent capture of objects by defining the frame of action.
One finding that further supports this interpretation is that distractors which onset prior to
the target captured visuospatial attention the most (compared with coincident with of
following). This suggests that attention was already distributed in parallel to multiple
locations in the visual field relative to the two action targets prior to the onset of the target
(Baldauf, et al., 2006; Meegan & Tipper, 1998; Tipper, et al., 1998).

A critical component of both of these findings was that distractors captured attention
more for grasp versus pointing reaches. This provides novel evidence that the attentional
priority placed on objects in actable space occurs relative to the goal of the action (and see
Tipper et al., 1997). This suggests that the top-down attentional selection prioritising
action-relevant objects interferes with how the action is executed. So for reaching to grasp, in addition to the suppression of affordances, there is also greater attentional prioritisation of objects that may pose obstacles to planned reaches.

One possible explanation for this prioritisation is that during grasping, non-task relevant distractors captured attention to a greater extent because grasp reaches required greater displacement of the digits compared with point reaches (Fernandez & Bootsma, 2004; Nordin & Frankel, 2001; Roy, et al., 2000; Schieber & Santello, 2004). This explanation is based on the proposition that perceptual systems evolved to facilitate action. Thus, the perceptual and attentional processes underlying the selection of action relevant inputs take account for the different composite parts of action execution to selectively prioritise certain inputs when they are relevant and suppress them when they are less so (Castiello, 2005; Goodale, 1990; Meegan & Tipper, 1998).

Findings from the second experiment similarly support the above proposition: reach types differed in their trajectories from one another based on the temporal relationship between the target and distractor. Namely, point reaches displayed the greatest deviations in reach trajectories for the distractors-following condition (relative to the preceding and coincident). Conversely, grasp reaches resulted in greater deviations in reach trajectories for both the distractor following and preceding conditions (relative to the coincident condition). The greater deviations for distractor-following conditions for both reach types indicate that compensatory corrections in reach trajectories occurred online to accommodate the onset of a stimulus within the frame of action following the development of an initial action plan. This suggests, consistent with previous research, that there was recalibration of the action plan, in real time, to enable the successful completion of the reach goal (Roy, et al., 2000).

With regards to peripersonal space, the current results correspond with the functional properties of hand-specific peripersonal neurons in premotor cortex. These display visuo-tactile receptive fields which represent visual objects relative to their proximity to the hand and continuously update their visual field during action (Duhamel, et al., 1998; Fogassi, et al., 1992; Graziano, 1999; Graziano & Gross, 1998; Rizzolatti, et al., 1996; Rizzolatti, et al., 1981). This is specifically the case for sub-populations within premotor cortex which code for goal-directed action and show greater activation for objects to be grasped versus gestured towards (Godschalk, et al., 1985; Rizzolatti, et al., 1996; Rizzolatti, et al., 1981). We have presented behavioural evidence that both target and non-target objects are coded in attention relative to their proximity to the hand, and the goals of manual actions.
In regards to the distribution of attention, evidence from human and primate research has found that reaching to grasp, versus merely reaching, selectively recruits the dorsal visual network (Binkofski et al., 1998; Colby & Goldberg, 1999; Culham et al., 2003; de Haan & Cowey, 2011; Goodale & Milner, 1992; Goodale, et al., 1991; Malach et al., 1995). Specifically, the anterior intraparietal (AIP) in the dorsal visual stream plays a critical role in processing objects properties required for grasp (Colby & Goldberg, 1999). Neuroimaging studies have found activation in AIP for visual objects, when observers grasp them but not when they merely reach towards them (analogous to the point condition in the current study). Accordingly, patient studies have found that damage to the AIP results in inabilities to scale the digits to successful grasp objects (Binkofski, et al., 1998; Culham, et al., 2003). This suggests that there are specific dorsal visual networks dedicated to processing vision for grasping, which most likely underlie the greater distractor prioritisation for grasp but not point actions found in the present study.

One factor which was not addressed in the current research was the direct relationship between visuospatial attention distribution and multisensory binding in peripersonal space. While the current findings provide evidence that attention works in combination with representation of peripersonal space processing of action-relevant visual objects, it is not directly clear what the directionality is between the two perceptual processes. That is, the remapping of peripersonal space during grasp may have driven the demonstrated effects in attention. Conversely the top-down attentional selection of action relevant stimuli drives the remapping of peripersonal space based on the goal of action. Our supposition is that it is the latter, based on evidence which suggests that top-down goals shape attention distribution which in turn facilitates multisensory integration (Theeuwes, 1991; Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2009). In line with this, we propose that goal-related shifts in attention drive the remapping of peripersonal space and not the reverse. Yet future research may seek to address this relationship more directly by investigating how neural networks recruited when distributing attention for action interface with those responsible for integrating near-body sensory inputs.

In conclusion, this study provides evidence that voluntary actions towards objects elicit changes in the distribution of visuospatial attention based on the action goal. Most importantly, we have shown that grasping reaches increase contingent capture and the activation of competing actions towards non target objects within the frame of action. These findings suggest that visuospatial attention plays a top-down role in shaping representation of peripersonal space to enhance selective processing of stimuli relevant to the execution of voluntary action, either objects being acted on, or those within the frame
of the action. Moreover they suggest that this may occur through a continuous updating of the spatial relations between target and non-target objects in action space.
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CHAPTER 5: GENERAL DISCUSSION
The overarching aim of the present thesis was to investigate how representation of the hands and action goals shapes visuospatial attention and in return how biases in visuospatial attention influence the processing of objects near the body. The described studies were designed to investigate specific bottom-up and top-down attentional biases with the aim of contributing to a cohesive understanding of the perception and action links which underpin human manual action. Previous research has shown that when visual objects are presented within perihand space, there are enhancements in processing of their magnocellular visual properties and faster shifts of spatial and temporal attention compared with objects outside of perihand space (Abrams, et al., 2008; Cosman & Vecera, 2010; Goodhew, et al., 2013; Gozli, et al., 2012; Reed, et al., 2010; Reed, et al., 2006). Similar biases in attention capture are also found for visual objects which appear within the frame of manual action (between the start and end point of a reach) (Tipper, et al., 1997; Tipper, et al., 1992; Welsh & Elliott, 2004; Welsh, et al., 1999). Yet, it remained unclear how the intrinsic functional properties of hands (their grasping capability) and the goals of manual actions themselves (how hands are used to interact with visual objects at a given time) specifically drive or impact such perceptual enhancements and attentional biases. Moreover, it was unclear how such top-down and bottom-up mechanisms work in combination to facilitate near-hand processing.

In the present thesis I began by examining how endogenous biases in visuospatial attention near hands impact on the processing of objects near the body. In the second study we extended upon this to investigate more directly how structural and functional differences in the body shape the selective processing of objects in the body’s immediate vicinity. Finally, the third study consolidated evidence from the first two studies to examine how concurrent exogenous and endogenous biases in visuospatial attention, specific to the hands, impacts how we process the immediate environment when engaged in dynamic action. Critically, the third study further extended understanding of near-body attention by examining how attentional modulations shape the resulting manual output.

**Overview of findings**

The first study (Chapter 2) investigated bottom-up modulations of attention, specifically regarding the impact of hand proximity on visual sensitivity for two types of magnocellular processing: luminance contrast sensitivity and object dimension judgement. With regards to luminance contrast sensitivity, observers detected sub-threshold, low contrast and high contrast luminance onsets. With regards to object dimension judgement, observers judged in which dimension a high contrast rectangular object was greatest,
width or height. Both magnocellular tasks were completed with the observer’s hands either adjacent to or distant from the visual display, in blocked trials. The results showed that whilst hand proximity did not impact luminance contrast sensitivity it did improve visual sensitivity for grasp-relevant visual stimulus properties. Importantly, this was only the case when targets were presented for long enough (longer than 200ms) to benefit from shifts of visuospatial attention prior to target offset.

The second study (Chapter 3), extended these findings to investigate how intrinsic differences in representation of the functional properties of hands influence covert shifts in exogenous visuospatial attention. It investigated the impact of handedness and the grasping capability (i.e. whether the palm or back of hand is oriented towards the stimulus) on directing visual attention near the body in a bottom-up manner. Left and right handed participants identified target shapes presented adjacent to or distant from their dominant or non-dominant hand. When the hand was aligned with the shoulder, object discrimination accuracy was enhanced for objects presented near the grasping surface of the right hand and impaired for those presented distant from it, irrespective of hand dominance. In addition, when hands were crossed over the body midline there were accuracy enhancements relative to the location, but not functional orientation of the right hand. Right handers also displayed speeded engagement and delayed disengagement of visuospatial attention for objects in the near-hand graspable location. These findings provide evidence of functional biases in near hand visual processing, relative to familiarity of use, when the hand in question was not directly acting on target objects. Moreover, they suggest that there is attentional prioritisation of graspable objects to the detriment of objects near the body but distant from the hand.

Finally, the third study (Chapter 4) extended upon the mere proximity research explored in Studies 1 and 2 and investigated top-down modulations of visuospatial attention during action. Specifically, I examined how the goals of manual actions (how an observer uses their hands to interact with visual objects) modify how visuospatial attention is directed towards visual objects in peripersonal space. Earlier research found that visual distractor objects within the frame of action (between the start and end point of a reach), activate competing actions (Welsh & Elliott, 2004) and capture visuospatial attention more than those outside the frame of action (Meegan & Tipper, 1998; Tipper, et al., 1997; Tipper, et al., 1992). In contrast, my focus was to investigate whether action goals modify the attentional priority given to distractors within the frame of action prior to initiation of any goal-directed action. If so, complex actions goals (grasping) should result in greater attention capture by distractors compared with simpler action goals (pointing). Observers
reached to point to or grasp target objects whilst presented with distractors within the frame of action. The results showed that when reaching to grasp a visual object, distractors within the frame of action captured visuospatial attention more than when reaching to point. Study 3 also examined the temporal dynamics of such spatial prioritisation (relative to onset of the action), by defining the point at which, during the course of action planning and execution, distractors most capture visuospatial attention (prior to, coincident with or following target onset). Visuospatial attention capture was enhanced for objects which onset after the target, compared with before or coincident with it. Moreover, changes in the visual environment which occurred after the onset of the target interfered with both the temporal and kinematic properties of action execution, such that there was greater response activation for non-target objects which onset after the reach had been planned.

**Implications of findings**

There are number of critical implications which stem from the work presented here. The first relates to the role that combined hand proximity and functional representation on the bottom-up allocation and shifting of visuospatial attention. The findings have also shown that manual action goals modulate the top-down distribution of visuospatial attention dynamically. That is, visuospatial attention is shifted within the frame of action relative to the type of reach being executed and the available visual information. This suggests that different aspects of manual representation impact distinct mechanisms of attention. Moreover, they indicate that improvements in basic magnocellular processing in the space near hands is likely due to greater allocation of visuospatial attention in the hands location, relative to manual action goals. Visuospatial attention is directed in a bottom-up manner based on the location and functional properties of hands but is also modified in a top-down manner during dynamic action relative to manual action goals. In addition, the findings demonstrate that top-down biases in visuospatial attention modify the response profiles of subsequent action demonstrating a direct relationship between visual perceptual biases and motor output. Taken together, the results provide evidence for a hierarchy of attentional biases which enhance perception of the action-relevant visual properties of objects near the hands which, in turn, guide the resultant manual output.

Previous behavioural research has shown that magnocellular perception is enhanced when visual objects are proximal versus distant from the hands. According to current accounts, such biases in visual processing are the result of selective recruitment of the dorsal visual pathway (as opposed to the ventral pathway) (Abrams, et al., 2008;
Dufour & Touzalin, 2008; Goodale & Milner, 1992; Goodhew, et al., 2013; Gozli, et al., 2014; Gozli, et al., 2012). The dorsal pathway is conceptualised as the perception for action pathway and as a result, demonstrable enhancements in the processing of magnocellular object properties are thought to reflect prioritisation of the action-relevant visual properties of near hand objects (Denison & Silver, 2012; Goodale & Milner, 1992; Goodhew, et al., 2014). That is, the action-relevant visual properties of hand adjacent objects are prioritised in perception and attention because they inform the generation of subsequent actions that will either involve the object itself or occur within the space that object/s are located.

This thesis has extended the understanding of near-hand magnocellular perception in a number of ways. First, the results indicate that hand proximity improves the perceptual processing of directly grasp-relevant magnocellular visual properties (object dimension judgements). This is evidence for early enhancements (< 250ms after target onset) in the processing of object properties which inform elements of manual action planning, such as grip scaling, based on the objects close proximity to the hands (Carnahan, Goodale, & Marteniuk, 1993; Castiello, 2005; Grafton, Fagg, Woods, & Arbib, 1996). Conversely, previous research has shown that grip scaling is relatively immune to the V-H Illusion (Aglioti, et al., 1995; Borchers & Himmelbach, 2012; Vishton, et al., 1999). The current work contributes to this by showing that improvements in the ability to scale one’s digits based on object dimensions most likely result from selective recruitment of the dorsal visual pathway prior to sensorimotor transformation. This extends upon earlier findings by demonstrating that mere hand proximity elicits similar reductions in the V-H illusion. Thus, the observer is able to identify the dimension of objects with precision near hands, in contexts where no grip scaling is required. The reductions in V-H Illusion found here, therefore imply that demonstrable prehensile reductions of the illusion (in the form of more precise grip scaling) likely reflect changes in visual perception rather than a result of a reduction or suppression of the bias during sensorimotor transformation.

Second, the present findings provide evidence that shifts in visuospatial attention contribute to the selective recruitment of the magnocellular visual stream to process near hand objects. In particular, they suggest that hand-specific attention biases (relative to location and functional properties) may drive such perceptual enhancements. Earlier near-hand attention research has also shown that the overall distribution of visuospatial attention is biased to hands location such that near hand objects are detected faster than those distant from the hand, irrespective of exogenous cues (Abrams, et al., 2008; Cosman & Vecera, 2010; Lloyd, et al., 2010; Reed, et al., 2006). These findings indicate
that there is covert attentional monitoring of the hands location. One likely function of this is to enhance detection of relevant candidates for action. In the present thesis, I consolidate these two disparate lines of research by demonstrating that hand-centred biases in the distribution and shifting of visuospatial attention likely drive lower-level visual perceptual changes such as magnocellular enhancements. The results showed that magnocellular enhancements only occurred visuospatial attention could be shifted to target objects prior to offset. These results indicate that hand location drives shifts in visuospatial attention which, in turn, enhance the processing of action-relevant visual inputs near hands.

In line with the above, a third implication of the current work is that the functional properties of hands (both with regards to their biomechanical grasping affordances and dynamic action goals) influence the extent to which visuospatial attention is biased to near-body objects. This is such that visuospatial attention is biased towards objects near the grasping surface of the right hand (particularly for right dominant individuals). Critically the results provide the first evidence of detriments in the identification of objects that onset in peripersonal space distant from the hand and which co-occur with enhancements near-hand processing. Conjointly, these findings indicate that it is more than just the relative location of hands which results in the selection of visual objects for further processing. Their subjective relevance to an action at a given time is also important. Moreover, such selective enhancements may co-occur with attentional suppression of other near-body objects that are distant from the hands.

These findings contribute to the existing literature because they provide further evidence of bottom-up biases in visuospatial attention relative to the internal representation of the hands. Further, results suggest that more frequent right hand usage may strengthen representation of its actionable properties and in turn drive attentional biases for objects in its vicinity (Amunts, et al., 1996; Gentilucci, et al., 1998b; Sörös, et al., 1999; Volkmann, et al., 1998). In turn, these results support the proposition that hand affordances enhance engagement of visuospatial attention to near-hand objects (Tucker & Ellis, 1998b; Vainio, Ellis, Tucker, & Symes, 2007; Vainio, Symes, Ellis, Tucker, & Ottoboni, 2008). This is particularly the case for right-handers, who not only display enhanced object identification but also faster engagement and slower disengagement of attention to near-hand objects.

A further implication of the current research pertains to differences in attentional representation of near-hand space between left and right handers. With the exception of research in which handedness was a particular variable of interest, to date near hand
research has recruited exclusively right-handed individuals. This is presumably based on existing evidence of structural and functional differences in neural representation of the dominant and non-dominant hands between left and right handers as well as behavioural differences in hand recognition (Amunts, et al., 1996; Buckingham, et al., 2011; Gentilucci, Daprati, & Gangitano, 1998a; Gentilucci, et al., 1998b; Le Bigot & Grosjean, 2012; Sörös, et al., 1999). Earlier research investigating handedness differences in visual sensitivity (for target location discrimination – a magnocellular visual property), found that left-handers do not display the mirror pattern of enhanced dominant-hand specific visual sensitivity that right handers do. Instead, evidence suggests that for left-handers visual sensitivity is enhanced for targets near either hand irrespective of laterality (Le Bigot & Grosjean, 2012). The current research extended this to show that there are also associated changes in the distribution of visuospatial attention between such groups, which also do not reflect a mirror image of the established visuospatial biases found for right handers. Critically, left-handed observers also displayed grasping space accuracy biases, but for their non-dominant hand. As outlined in Study 2, these may reflect use-specific changes in representation, resulting from acting within environments in which many objects are designed to afford action for the right hands. Moreover, when the current findings are considered in combination with the results of Le Bigot and Grosjean (2012), they suggest that whilst left-handers may have lower-level visual sensitivity enhancements for objects near both the dominant and non-dominant hand, these do not directly result in changes in the shifting of visuospatial attention. This implies that structural and functional differences between left and right handers in the sensory representation of hands contributes to bottom-up attentional mechanisms, and are impacted by use-specific factors.

With regards to top-down attentional modulations, the present research has shown that action goals modify the distribution of visuospatial attention. Specifically, grasp versus point actions enhance attention capture of within-action-frame distractors and such attentional capture shapes subsequent motor output. Distractors within the frame of action are prioritised based on their position within the frame of action, as well as relative to action demands. That is, biomechanically complex action-goals (grasping) facilitate greater perceptual prioritisation of non-target visual objects relative to less complex ones (pointing). The findings also indicate that such top-down attentional prioritisation has a direct impact on the trajectories of executed actions (motor output). One possible explanation for the over-avoidance of non-target distractors during grasp (versus point) reaches is that grasp reaches required greater digit manipulation (grip scaling) compared with point reaches (Fernandez & Bootsma, 2004; Nordin & Frankel, 2001; Roy, Paulignan,
Farnè, Jouffrais, & Boussaoud, 2000; Schieber & Santello, 2004). As a result, greater top-down attentional prioritisation of non-target objects may occur because they represent obstacles to the reach path, or influence grip scaling at a more distal point in the reach, when grasping versus pointing. In turn, the greater deviations in the subsequent trajectories of grasp reaches are likely a reflection of this potential obstacle avoidance. That is, over-avoidance precludes non-target objects from becoming obstacles to the completion of the action goal (Castiello, 2005; Goodale, 1990; Meegan & Tipper, 1998).

Importantly, the current findings have also shown that enhanced attentional capture occurs relative to available visual information during action planning, but that the kinematics of actions reflect an updating of perceptual priority placed on non-target distractors. Specifically, point and grasp reach trajectories differed depending on to the temporal relationship between the target and distractor. For point reaches, the largest trajectory deviations were for the distractor-following condition (relative to the preceding and coincident). By contrast, grasp reaches resulted in larger trajectory deviations for both the distractor-following and -preceding conditions (relative to the coincident condition). Increased reach deviations for both reach types in the distractor-following condition provides evidence for compensatory which occur online (after the development of the initial reach plan). Thus there is evidence of trajectory recalibration which occurs in real time to facilitate successful execution of the reach goal.

In combination with earlier multisensory integration and crossmodal attention research, the present findings show a bidirectional relationship between the multisensory representation of the body, and visual perception (Macaluso & Driver, 2001; Macaluso & Maravita, 2010; Maravita, et al., 2003). The results suggest that hands bias shifts in visuospatial attention and that attentional prioritisation may contribute to selective engagement of the dorsal visual network. Moreover, the present findings indicate that intrinsic representation of the body influences properties of visual perception and in addition, action goals modify the selection for further processing of visual inputs. This pattern of results is consistent with both the embodied and integrative theories of perception and action because they reflect both perceptual changes relevant to action goals, and changes in motor output relative to available visual input (Bridgeman & Tseng, 2011; Gibson, 1979).

With regards to the hierarchy of near hand attention biases, this thesis has shown, first, that hand proximity enhances visuospatial attention within the perihand zone and this is associated with improvements in grasp-relevant magnocellular processing. Second, visuospatial enhancements are driven in a bottom-up manner based on the relative
location and affordances of hands themselves. That is, they are faster when objects are grasprable or near the dominant hand. Third, action goals shape the affordances of objects near the body. Consequently, objects near the body capture visuospatial attention to a greater extent when the actor must execute complex object based actions, compared with simpler goal directed actions. This suggests that whilst hand proximity and functional representation drives bottom-up shifts in visuospatial attention, manual action goals may serve to override the effects of these and facilitate top-down shifts in visuospatial attention based on the dynamic requirements of actions.

More broadly, the current thesis contributes to a greater understanding of the mechanistic links between perception and action. With regards to the embodied theory of cognition, the collective findings demonstrate that the fundamental structure of the hands shapes how environmental stimuli are selected and subsequently processed in the visuomotor system. The findings show that mere proximity of hands is sufficient to enhance the perceptual processing of action relevant inputs from environmental input. In this way we have demonstrated bi-directional links between the structure and function of the body, and the perceptual processing of stimuli arising from the environment around us. This is consistent with the theoretical perspective that both lower level perceptual processing and higher order cognitive functions are bounded in bodily states (Bridgeman & Tseng, 2011). Thus, understanding of the structure and function of the body, contributes to understanding of environmental processing.

The current thesis further extends on theoretical understanding of perception and action links by directly investigating how attentional processes adapt when hands are engaged in dynamic goal-directed action. Specifically, we have shown how exogenous attention capture helps to facilitate identification of potential obstacles, and that endogenous (goal-directed) attention contributes to the suppression of irrelevant objects near the body. The result of these concurrent processes is that the trajectory of subsequent action is streamlined. Critically, the current work shows that that attentional processes occur online to facilitate changes in motor output which reflect changes in task demands that arise from changes in the visual environment.

**Limitations and future research**

The current research presents a number of directions for further investigation. Foremost among these is need to establish the directionality of the relationship between hand-centred visuospatial attention biases and associated enhancements in magnocellular perception in the perihand zone. From the current results it appears that shifts in
visuospatial attention contribute substantially to enhancements in magnocellular processing. One candidate explanation is that visuospatial attention is biased to the hands location, relative to manual action goals which facilitates the selective recruitment of the dorsal visual pathway to enhance processing of action-relevant visual object properties. An alternative explanation is that hand proximity boosts the signal of magnocellular inputs pre-attentively, and such enhancements benefit from combined signal enhancement and near-hand biases in visuospatial attention. Yet, the neural mechanisms directly linking near-hand visuospatial biases and magnocellular enhancements remain unclear. Electrophysiological and neuroimaging research may clarify this by elucidating the temporal relationship between attention related neural activation and visual cortex activation and the functional connectivity between the regions responsible for each when visual objects are presented near hands.

Further research is also required to establish the temporal constraints of basic near-hand enhancements in contrast sensitivity, and to identify whether the attentional mechanisms responsible for these are dissociable from those responsible to object dimension judgment enhancements. Specifically, there remains a need to establish whether longer stimulus presentations do indeed elicit near-hand enhancements in luminance contrast sensitivity. The candidate explanation for the lack of near-hand luminance contrasts sensitivity enhancements in the first study, is that luminance onsets, particularly for threshold contrasts, do not benefit from near hand shifts in attention when presented for 250ms or less. Yet, Dufour and Touzalin (2008) found evidence for near-hand luminance contrast sensitivity enhancements for stimulus presentations of 500ms. Thus, contrast sensitivity may benefit from longer stimulus presentation, and as a result greater allocation of attentional resources, especially for low and sub-threshold contrasts. Previous findings show that shifts in covert visuospatial attention enhance the signal of luminance contrasts at the site of the attention shift (Carrasco, et al., 2000; Yeshurun & Carrasco, 1998). In line with this, longer (+250ms) stimulus presentations may be required to elicit any perceptual enhancements. Thus, an important direction for future research is to determine the temporal threshold for such near-hand luminance contrast sensitivity enhancements. That is, to establish when within the 250ms – 500ms window, hand proximity begins to elicit enhancements in luminance contrast sensitivity. Such research would allow insight into the time-course of near hand attention shifts and further contribute to understanding of the relationship between near hand visuospatial attention biases and basic magnocellular processing.
Another question which arises from this research relates to the bidirectional relationship between top-down visuospatial attention biases and changes in the multisensory representation of near-body space during manual action. Current understanding of near body processing is that there are feed-forward and feedback links between neural regions responsible representing the multisensory space near the hands and those responsible for distributing attention (Eimer, 2001; Eimer & Driver, 2001; Eimer, Velzen, & Driver, 2002; Macaluso, Frith, & Driver, 2005; Macaluso & Maravita, 2010; Spence & Santangelo, 2009; Talsma, et al., 2010). Moreover, representation of the limbs and the coordination of subsequent motor output relies intrinsically on the combination of proprioceptive and tactile limb centred inputs with near body, and limb centred visual inputs (Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009; Holmes & Spence, 2004; Maravita, et al., 2003; Tsakiris, Schütz-Bosbach, & Gallagher, 2007). For example, the behavioural findings of Brozzoli et al., (2010; 2009) indicate that reaching to grasp versus point to an object results in visuotactile integration between object centred visual inputs and hand-centred tactile inputs, during but not prior to action execution. The results of the current thesis provide convergent evidence for online changes in visuospatial attention capture which occur prior to action onset, based on action goals. Importantly, the greatest attention capture was found for distractors presented prior to action planning (onset of the target) indicating that changes in visuospatial attention occur prior to action onset. Thus, updating distributions of visuospatial attention may in turn drive updating of multisensory representation of near body space, relative to changing action goals. Yet, based on the present findings, it is not directly clear what the directionality is between the two perceptual processes. Neuroimaging research may seek to address this relationship more directly by investigating how neural networks recruited when distributing attention for action interface with those responsible for integrating near-body sensory inputs.

**Conclusions**

The current thesis presents novel evidence regarding the bidirectional relationship between internal representation of hands and near-hand visual processing. The results revealed that the functional properties of hands, and manual action goals modify near-body visual processing systematically (both at basic perceptual levels and with regards to attention). Moreover, the thesis provides evidence that such systematic enhancements in visual perception and attention impact the planning and execution of manual action and account for changes in the visual environment online. Together, the research presented here contributes to a broader understanding of perception in that it shows that near hand visual perception is intrinsically modified by the actable properties of objects and the hands
themselves, and is shaped by a hierarchy of attentional mechanisms, which facilitate manual action.
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APPENDIX A: SUPPLEMENTARY ANALYSES FOR CHAPTER 4
Timing parameters

Initiation times that were < 200ms (anticipatory < 1% of trials) and > 2000ms (not stimulus driven <3% of trials) were removed from the analysis. As with the first experiment, we computed the reach initiation cost by subtracting the no distractor initiation time from each of the distractor side (same side; opposite side) initiation time for each of the SOAs. Thus, mean initiation time was assessed using a 2 Reach Type (Point, Grasp) x 2 Target Location (left, right) by 2 Visual Distractor Side (same-side reach initiation cost and opposite-side reach initiation cost) repeated measures ANOVA.

In line with Experiment 1 there was a main effect of Distractor Side ($F(1, 17) = 5.99$, $p = .026, \eta_p^2 = .26$) which revealed that participants had a smaller reach initiation cost for same-side ($M = 12.45, SD = 5.87$) versus opposite-side distractors ($M = 27.18, SD = 8.84$). This provides further support for the proposition that visuospatial attention was captured by objects within the frame of action and thus there was a greater cost associated with shifting visuospatial attention from one hemifield to the other to attend to the target and plan subsequent actions.

A main effect of SOA ($F(2, 34) = 11.15$, $p < .001, \eta_p^2 = .40$) revealed that participants had a smaller reach initiation costs when there was zero SOA between the target and distractor ($M = -3.02, SD = 26.11$) compared with -200ms ($M = 51.89, SD = 64.09$) or +200ms distractors ($M = 10.57, SD = 20.89$; $t(17) = 3.60, p = .002$ and $t(17) = 2.91, p = .010$ respectively). In line with our prediction, participants also had smaller reach initiation costs when the target appeared +200ms compared with -200ms ($t(17) = 3.02, p = .008$). This was expected, and consistent with the first hypothesis that distractors which onset after the target would be suppressed in attention and thus initiation times would be minimally affected by attention shifts to the distractor location.

In line with our prediction, -200ms distractors delayed reach onset relative to both coincident and +200ms distractors. This implies two possibilities. First, it suggests that there is an overall temporal bias in shifting of visuospatial attention from the distractor to the target. Second it indicates that distractors within the frame of action captured attention more so when they appeared before the target than coincident with or following the target. This is possibly because participants were unaware which target they were grasping towards and attentionally prioritised both distractors within the display. One unexpected findings was the smaller cost associated with the coincident condition compared with the +200ms following condition indicating more delayed reaches when the distractor onset after the target. However, this finding may also be explained in terms of perceptual
uncertainty resulting from task demands. When there was no associated distractor at the
target onset, the trial could still have been a no distractor trial and participants reaches
may have been delayed due to this perceptual uncertainty until the later onset of the
distractor. This finding then further supports the explanation that shifts of attention to
following distractors are suppressed because participants took longer to initiate the reach
until the perceptual uncertainty was resolved by the onset of the distractor.

The two main effects were further clarified by an interaction between SOA and
Distractor Side \( (F(2, 34) = 5.47, p = .009, \eta^2_p = .24) \). This revealed that for same side
distractors, participants had a smaller reach initiation costs when there was no SOA \( (M = -6.09, SD = 26.98) \) compared with -200ms \( (M = 48.73, SD = 52.63; t(17) = 4.14, p < .001) \). They also had a smaller reach initiation cost when same-side distractors illuminated
+200ms \( (M = -6.35, SD = 23.24) \) compared with -200ms \( (M = 48.73, SD = 52.65; t(17) = 4.08, p = .001) \). For opposite-side distractors, participants had a smaller reach initiation cost when there was no SOA \( (M = -1.57, SD = 28.12) \) compared with -200ms \( (M = 55.14, SD = 81.45; t(17) = 2.89, p = .011) \) and compared with +200ms \( (M = 27.86, SD = 35.12; t(17) = 3.48, p = .003) \). These findings indicate, in line with those from Experiment 1, that
distractors capture visuospatial attention when within the frame of action. Further they
contribute to the main effects by illustrating that there are greater costs associated with
shifting attention to the target location when distractors are both temporally (onset prior to
or following the target) and spatially displaced (appear in the opposite hemispace) from the
target location.

There was also a 3-way interaction between reach type, SOA and target side \( (F(2, 34) = 6.14, p = .005, \eta^2_p = .27) \). For pointing trials, participants had a significantly smaller
reach initiation cost with left sided targets when the distractor onset coincidentally with the
target \( (M = -.77, SD = 39.89) \) compared when in onset -200ms \( (M = 43.74, SD = 81.35) \)
\( t(17) = 2.75, p = .014 \). They also showed this same pattern with right-sided targets (0ms:
\( M = -8.71, SD = 56.44; -200ms: M = 64.49, SD = 93.08, t(17) = 3.69, p = .002) \). There was
also a significantly smaller reach initiation cost for pointing trials with right sided targets
when the distractor onset +200ms after \( (M = 23.01, SD = 52.10) \) versus -200ms \( (M =
43.74, SD = 81.35; t(17) = 2.81, p = .012) \). For grasping trials there was also a significantly
smaller reach onset for left sided targets when the distractor onset coincidentally with the
target \( (M = -17.30, SD = 37.92) \) compared with -200ms \( (M = 51.33, SD = 61.83) \) \( t(17) =
5.17, p < .001 \). There was also a significantly smaller reach initiation cost for left sided
targets when the distractor onset +200ms \( (M = -11.01, SD = 43.69) \) versus -200ms \( (M =

51.33, $SD = 61.83; t(17) = 3.98, p = .001)$. Thus the largest reach onsets were found for the -200ms conditions for point reaches irrespective of the target location. They also reveal the same pattern for grasp reaches but only for left sided targets.

There was a further 3-way interaction between SOA, target side and distractor onset ($F(2, 34) = 9.43, p = .001, \eta_p^2 = .36$). For left-sided targets, participants had a smaller reach initiation cost for same-side distractors when they onset coincident with the target ($M = -10.36, SD = 31.90$) compared with -200ms ($M = 37.38, SD = 57.51$) $t(17) = 3.99, p = .001$. There was also a smaller reach initiation cost when the same-side distractor onset +200ms ($M = -5.98, SD = 38.24$) compared with -200ms ($M = 37.38, SD = 57.51$) $t(17) = 2.84, p = .011$. For left sided targets there was also a smaller reach initiation cost for opposite-side distractors which onset coincident with the target ($M = -7.71, SD = 39.99$) compared with -200ms ($M = 57.69, SD = 81.50$). There was also a smaller reach initiation cost for opposite sided distractors which onset +200ms ($M = -20, SD = 39.48$) compared -200ms ($M = 57.69, SD = 81.50; t(17) = 2.73, p = .014$). For right sided targets there was a smaller onset cost when same-side distractors onset coincident with the target ($M = 1.83, SD = 42.76$) compared with -200ms ($M = 60.08, SD = 60.52; t(17) = 3.98, p = .001$). There was also a smaller cost for +200ms ($M = 60.08, SD = 60.52) t(17) = 4.68, p < .001$. Finally for opposite side distractors there was a smaller reach initiation cost when they appeared coincident with ($M = 4.57, SD = 39.37$) versus -200ms ($M = 55.91, SD = 62.00) t(17) = 3.03, p = .008$. These findings indicate that for both left and right targets, the smallest reach initiation costs were for the coincident condition, followed by the following condition and the largest reach initiation cost were for the preceding condition.

**Reach trajectories**

Deviations along the x-axis were investigated by assessing the maximum positive deviation along the x-axis. Because we were interested in investigating how the timing of distractors influenced reach trajectories we compared SOAs (0ms, -200ms and +200ms) using a 2 reach type (point, grasp) by 2 target location (left, right) by 2 distractor side (same-side, opposite-side) $^4$ ANOVA.

**Reach type and target location.** A main effect of Reach Type $F(1, 17) = 21.26, p < .001, \eta_p^2 = .56$ revealed that, consistent with the findings of experiment 1, participants deviated more when they were grasping ($M = 26.88, SE = 1.33$) versus pointing to the

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$^4$ Because the no-distractor condition was the same for each of the SOAs, this was not included in the calculation of the omnibus ANOVA as we aimed to compare distractor effects between SOAs.
targets ($M = 24.67$, $SE = 1.79$). Also consistent with experiment 1, there was a main effect of target location ($F(1, 17) = 8.82$ $p = .017$, $\eta_p^2 = .29$), whereby participants deviated more positively when reaching to right targets ($M = 29.21$, $SD = 2.18$) versus left targets ($M = 22.34$, $SD = 1.46$).

A reach type by target location interaction ($F(1, 17) = 10.84$ $p = .004$, $\eta_p^2 = .40$) shows that participants deviated less when grasping left ($M = 22.79$, $SD = 6.30$) versus right targets ($M = 30.98$, $SD = 9.68$) $t(17) = 2.94$, $p < .001$. These findings are consistent with those found in experiment 1 in regards to greater deviations along a natural trajectory for grasp versus point reaches.

SOA interactions. An interaction between reach type and SOA ($F(1, 17) = 33.65$, $p < .001$, $\eta_p^2 = .66$) revealed that participants deviated more for $+200$ms ($M = 29.21$, $SD = 5.32$) compared with coincident with the target ($M = 21.89$, $SD = 6.08$; $t(17) = 8.04$, $p < .001$) or $-200$ms ($M = 22.90$, $SD = 6.62$; $t(17) = 7.03$, $p < .001$). For grasping reaches, this pattern was slightly different: participants deviated more for $-200$ms ($M = 29.21$, $SD = 5.61$) and $+200$ms ($M = 28.62$, $SD = 5.67$) compared with the coincident condition ($M = 22.82$, $SD = 6.50$; $t(17) = 8.16$, $p < .001$ and $t(17) = 6.41$, $p < .001$ respectively).

An interaction between target location and SOA ($F(1, 17) = 13.27$ $p < .001$, $\eta_p^2 = .44$) revealed that for left sided targets, participants deviated more when the distractor onset $+200$ms ($M = 24.26$, $SD = 6.74$) compared with coincident with the target ($M = 23.97$, $SD = 9.03$) or $-200$ms ($M = 22.02$, $SD = 6.75$; $t(17) = 3.60$, $p = .002$ and $t(17) = 3.13$, $p = .006$ respectively). For right sided targets, participants deviated more when the distractor onset $-200$ms ($M = 30.09$, $SD = 9.47$) and $+200$ms ($M = 33.57$, $SD = 10.19$) compared with the coincident condition ($M = 23.97$, $SD = 9.03$; $t(17) = 8.33$, $p < .001$ and $t(17) = 7.24$, $p < .001$ respectively). Reach trajectories also deviated more for $+200$ms compared with $-200$ms $t(17) = 4.19$, $p = .001$. In line with prediction, reaches deviated to a greater extent when the distractor onset after the target compared with coincident and before it, for both left and right target locations which reflect greater obstacle avoidance. There was also a three-way interaction between reach type, SOA and target location $F(1, 17) = 5.02$ $p = .012$, $\eta_p^2 = .23$. For pointing trials, participants deviated more for left sided targets when the distractor onset $+200$ms ($M = 24.99$, $SD = 7.14$) compared with the coincident ($M = 20.14$, $SD = 5.43$) and $-200$ms ($M = 20.55$, $SD = 6.76$; $t(17) = 4.19$, $p = .001$ and $t(17) = 4.60$, $p <
Participants also deviated more for right targets when the distractor onset +200ms ($M = 33.44, SD = 10.18$) compared with the coincident ($M = 23.63, SD = 9.25$) and -200ms ($M = 25.25, SD = 9.35; t(17) = 7.03, p < .001$ and $t(17) = 75.46, p < .001$ respectively). For grasping trials, reaches deviated more for right sided targets when the distractor onset -200ms ($M = 34.93, SD = 10.85$) or +200ms ($M = 33.70, SD = 10.78$) compared with the coincident condition ($M = 24.30, SD = 9.10; t(17) = 6.57, p = .001$ and $t(17) = 6.00, p < .001$ respectively).